Sediment-algal interactions on intertidal rocky reefs

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Tania Dianne Hurley

UNIVERSITY OF CANTERBURY
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Abstract

Macroalgae are a dominant feature of many rocky intertidal habitats worldwide. An understanding of the processes affecting their growth and survival, especially at early life history stages, is therefore important to an understanding of the structure of rocky intertidal communities. This thesis examines the role that the sediment environment has on habitat-dominating fucoid algae and intertidal community structure. Measurements of sediment flux showed considerable spatial and seasonal variation, while the benthic sediment environment remained relatively stable. Experimental disturbances over 13 months, showed two distinct effects. First, direct effects of sedimentation favoured ephemeral algae and also those with tough thalli. Secondary to this was an alteration of species interactions due to the shifts in community composition.

The effect sedimentation has on habitat dominating fucoid algae was also examined with laboratory experiments and outplants of cultured algae. The presence of sediment had a negative effect on the ability of *Cystophora torulosa* and *Hormosira banksii* zygotes to attach to the substratum, with even sparse coverings of sediment preventing at least 37% of zygotes attaching to the substratum, and almost a complete recruitment failure with dense coverings of both sand and silt. Sediment and disturbance of turfing communities also influenced early post-settlement survival especially of *C. torulosa*.

Manipulations of the sediment load, nutrient levels and grazer abundance showed the resilience of rocky intertidal communities to the predicted increase in nutrient leaves in coastal waters due to increases anthropogenic intrusion.

Most research into the effects of sedimentation have been observational studies and much of the experimental work has been carried out subtidally. My experiments have extended research into the intertidal zone, finding that if sedimentation increases as predicted there will be a consequential loss of habitat dominating fucoid algae and its replacement with sediment tolerant species.

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Chapter 1. General Introduction

1.1. Introduction

Macroalgae are a dominant feature of many rocky intertidal habitats worldwide and are important ecological, economic and cultural resources (Schiel & Foster 2006). An understanding of the processes affecting their growth and survival, especially at early life history stages, is therefore important to an understanding of the structure of rocky intertidal communities. This thesis examines the role that the sediment environment has on habitat-dominating fucoid algae and intertidal community structure. There is a need for researchers to quantify the effects of sedimentation and identify critical threshold levels to underpin sustainable coastal management polices (Airoldi 2003). This is complicated by a need to distinguish between anthropogenic impacts and natural variability in sediment flux (Turner 2004). Key questions are 1) how does sedimentation affect biotic interactions and community structure, 2) how do other disturbances affect these interactions in the intertidal zone and 3) how variations in the sediment environment both in amount and composition, influence the recruitment and survival of habitat-dominating macroalgae.

1.1.1 Sedimentation

Increased sedimentation is a threat to marine biodiversity (Thrush et al. 2004), especially in rocky intertidal habitats, where dramatic alterations to the benthos can occur (Airoldi 2003). This threat is recognized at the highest levels, with the United Nations Environmental Program listing sedimentation as a threat to marine ecosystem function (Unep 1995). The major sources of natural sedimentation include river discharge, erosion of cliffs, and along-shore sediment transport (Chien & Wan 1999). Sediments from anthropogenic sources reach rocky shores through a range of these natural sources, but have different volumes and characteristics such as the size and chemical composition of the particles (Airoldi 2003). Increased sediments from anthropogenic sources come from direct discharge, construction and dredging, or more typically, from an acceleration of the natural sedimentation regime (Ritter et al. 2002). One common cause of increased sedimentation is the conversion of forests into pastoral land, which increases erosion of top soils (Airoldi 2003). Land conversions have been shown consistently to dramatically increase sediment yields in adjacent waterways. In the US Virgin Islands, for example deforestation, has led to a 4-fold increase in sediment yields in coastal waters (MacDonald et al. 1997). The sediment

environment may also be altered as a result of climate change, as soil erosion increases with changes to the hydrological cycle (Nearing et al. 2004).

Large fluctuations in the sediment environment are not solely attributable to anthropogenic causes; natural weather phenomenon can have great effects on rocky shores. Sediment flux during storms is often several orders of magnitude higher than natural ambient rates, and can last for hours or days depending on storm intensity and lag effects (Airoldi 2003). The large volumes of water passing through river systems during flooding reduces the retention efficiency of sediment catchments (e.g., estuaries) which in turn increases the sediment load reaching coastlines (Eyre et al. 1998). For example, during a 20 year period, flood sediment load increased 3-fold in a subtropical Brisbane estuary due to land surface flooding carrying sediment into the catchment. With such a large volume of water passing through the estuary, 77% of this sediment was exported to adjacent bays (Eyre et al. 1998). Significant sediment discharge due to extreme weather events has also been recorded in New Zealand. In 1988, cyclone Bola, a putative once in 100 year storm, caused an increase in sediment discharges from the Waipaoa River, (Hawke's Bay, North Island New Zealand) in excess of 40 million tonnes. This was 3-4 times the annual sediment yield (Page et al. 1999).

The spatial and temporal distribution of sediments is highly variable (Airoldi 2003). At the largest scale, the distribution of sediment is influenced by seasonal and tidal cycles (D'Antonio 1986). Seasonal trends are variable between locations with some studies reporting higher rates in summer (Littler et al. 1983) and others in autumn/winter (Airoldi et al. 1996) The size distribution of sediments also varies over several spatial scales. Larger grain sizes settle out of suspension close to the source, whereas smaller particles will travel longer distances, especially under turbulent conditions (Moore 1972). Once the transport processes have acted to bring sediment to a location, site exposure plays an important role in sediment distribution. Sediments are more likely to accumulate at sheltered locations where the chance of resuspension is low (D'Antonio 1986). Conversely, in exposed locations, sediment is often trapped in cracks, crevices or in benthic organisms (Airoldi & Virgilio 1998). On the finest scale, the within-shore distribution of sediment is highly influenced by microtopography and local current flows (Chien & Wan 1999): for example, sediments are more likely to accumulate on horizontal surfaces than on slopes (Whorff et al. 1995).

Sedimentation is not simply the arrival of sediment at a site but is clearly influenced by biological factors. For example, mussels and turfing algae cover the substratum and can trap and bind sediments (Airoldi 2003). Algal turfs can be extensive over large spatial scales despite their tendency to be overgrown by other benthic species (Airoldi 2000), and are found

in both temperate and tropical regions, in subtidal and intertidal zone (Hay 1981, Adey & Goertemiller 1988, Kendrick 1991). In recent times, the spatial dominance of turf has been reported to be increasing (Airoldi & Cinelli 1997). This has been attributed to an increase in the disturbance rate in coastal areas (Seapy & Littler 1982). There has been little research on the effects of sediment on turfing communities (Irving & Connell 2002), despite the fact that sediment is considered a structural constituent of many turfing algae (Stewart 1983, Kendrick 1991, Airoldi & Cinelli 1997, Airoldi 2003). An understanding of turf-sediment interactions is not only important for predicting the effects of increased sedimentation, but also for understanding the processes that maintain heterogeneity in turf-dominated habitats (Irving & Connell 2002).

Previous research has focused on characterising sediment–turf interactions in shallow subtidal habitats (Airoldi et al. 1996, Airoldi 1998, Airoldi & Virgilio 1998, Airoldi 2003). The effect sediment has on the biomass and cover of turfing algae has been variable. Experiments along Mediterranean coasts have shown that sediment deposition affects the biomass of the turf (Kendrick 1991, Airoldi & Cinelli 1997), but not its overall percentage cover (Airoldi & Virgilio 1998). However, subtidal experiments along the Australian coast suggest that increased levels of sediment negatively affect both the biomass and cover of turfing algae (Irving & Connell 2002). Turf-forming algae may play an important role in mediating effects of sedimentation. Airoldi and Virgilio (1998) showed that subtidal turf assemblages bind sediments, allowing a constant covering of sediment despite variation in the flux of sediment. The entrapped layer of sediment bound in turfs has been proposed as a mechanism by which turfs maintain their spatial dominance by inhibiting recruitment of non-turfing algae (Sousa 1984, D'Antonio 1986). This research now needs to be extended into the intertidal zone where the turbulent nature of the environment may alter previously identified interactions (Gaylord 1999).

Although there has been much interest in the effects that increased sedimentation can have on rocky shore communities, there is a lack of understanding of what mechanisms underlie the observed patterns (Airoldi 2003). Airoldi (2003) found the main effects sediments have on rocky shores are changes in species composition and distribution, inhibitions of settlement and recruitment, and loss of species. Airoldi's review (2003) on the effects of sedimentation suggested three major mechanisms by which inorganic sediments can affect rocky shore species: 1) burial/smothering, which can reduce availability of vital resources such as light, oxygen and nutrients and, if it continues for extended periods of time, anoxic microenvironments may develop; 2) scour and/or abrasion, which can remove whole

organisms or significant proportions of their biomass (Airoldi & Virgilio 1998) and is particularly important at sites that have high current velocities and where larger grain sizes dominate; 3) changes to the physical characteristics of the substratum as a result of a change from stable hard bottom to unstable soft sediments. These effects are not mutually exclusive and may interact so it is important to identify their relative contributions (Airoldi 2003).

Despite the interest in the effects of sedimentation there has been no consensus in the literature on how sedimentation affects community structure. This is due to the extensive spatiotemporal variation in the sediment environment across wide spatial scales from centimetres to kilometres (Airoldi et al. 1996), and the interactive effects of sedimentation with biotic communities. A body of literature suggests that increases in sedimentation on rocky shores will decrease richness and diversity of communities (Daly & Mathieson 1977, Salinas & Urdangarin 1994, Airoldi & Virgilio 1998). However, on shoreline scales, diversity may be enhanced by sedimentation, as communities become a mix of sand tolerant species and the original rocky shore community (Thompson et al. 2002) due to the spatial and temporal variation in the deposition of sediment (Littler et al. 1983).

1.1.2 Disturbance in the Marine environment

Disturbance is ever-present in the rocky intertidal zone (Emerson & Zedler 1978), including waves, extreme weather events and increasing human impacts (Schiel 2004). Anthropogenic disturbances can interact with ecological processes varying across spatial and temporal scales, resulting in alterations to relative abundances and composition of communities through direct and indirect effects (Benedetti-Cecchi et al. 2001). In densely colonised environments such as the rocky intertidal zone (Airoldi & Virgilio 1998), disturbance is the main mechanism that creates primary space (bare rock) allowing the expansion of existing species and recruitment of new species (Sousa 1984). Disturbances can lead either to a diverse coexisting assemblage of species or dominance by a few tolerant species (Airoldi 1998). Subtidal disturbance and sediment experiments have shown the significant influence that the timing, intensity and size of disturbance have on recolonisation of turfing algae (Airoldi 1998). Sediment may alter the patterns of succession after a disturbance due to differential abilities of species to recruit under different sediment environments. Kendrick (1991) found in a subtidal lagoon that crustose coralline algae colonized bare surfaces when sediment was removed, but under natural sediment rates filamentous algae were the early successional species. Sediments can also fill cracks and

crevices, which under ambient conditions can provide refuge from disturbance (Airoldi 1998, Airoldi & Virgilio 1998). Balata (2007a) found that sedimentation reduced the dissimilarity between assemblages, removing the influence of substrate heterogeneity and reducing beta (between site) diversity.

Increased sedimentation can also be associated with other forms of physical disturbance, both natural (e.g. removal of biomass by extreme weather events) and anthropogenic (e.g. trampling), and these can affect both the canopy and turfing algae. Because the benthic sediment environment is greatly influenced by the structure of the turfing community (Airoldi 2003), any removal of biomass, either partial or complete, can alter the sediment environment and biotic interactions between turfing algae and other species. Sediments can not only interact with physical disturbances, but can alter the chemical properties of water and benthic sediment environment. Sediment from anthropogenic sources, especially when associated with agricultural runoff, can cause eutrophication of coastal waters (Thompson et al. 2002).

1.1.3 Early life history of algae

The patterns of survival of algal propagules in the period between settlement and recruitment underlie the patterns seen in adult populations (Norton 1983, Underwood et al. 1983). The early life history stages of algae are subject to a wide variety of abiotic and biotic stresses (Santelices 1990, Valdas et al. 1992, Schiel & Foster 2006), which interact with each other and vary in space and time (Dunmore 2006). Vadas (1992) listed 17 extrinsic and 6 intrinsic factors that can influence post-settlement survival. Extrinsic factors include species interactions, substratum type and the physical environment. Intrinsic factors include attachment time, growth rates and viability. The sediment environment will likely interact with some or all of these extrinsic and intrinsic factors to influence post-settlement survival. Previous research done on intertidal platforms around Kaikoura (South Island, New Zealand) has shown that the growth and survival of the early life history stages of habit dominating fucoid algae are influenced by a wide range of these factors including, tide height, shading, grazing and sediment load (Dunmore 2006, Schiel 2006, Schiel & Lilley 2007).

1.1.4 Fucoid Algae

Numerous studies have shown the importance of canopy-forming algae in structuring intertidal communities via both positive (Bertness et al. 1999, Irving et al. 2004) and negative interactions (Schiel 2006). The dominant canopy-forming algae on moderately sheltered southern New Zealand coasts are fucoid algae (Schiel 2004, 2006, Schiel & Foster 2006). *Hormosira banksii* dominates the mid shore and *Cystophora torulosa* the lower shore. Removal of the *H. banksii* canopy causes a burn-off in coralline algae, blooms of ephemeral algae and an overall decline in diversity for at least two years (Lilley & Schiel 2006). The most immediate effect is the loss of micrograstropods that live amongst the canopy (Lilley & Schiel 2006). Canopy species can positively influence understory species by altering the physical environment. Alterations include reduced light reaching the substratum (Reed & Foster 1984), increased abrasion (Irving & Connell 2006) and amelioration of physical extremes (McCook & Chapman 1991). Because of the importance of fucoid algae, an understanding of the factors influencing their survival, especially as juveniles, is necessary to understand the maintenance of community structure, even more so in a time when anthropogenic stress is increasing. Differences in specie's life history traits can alter recruitment patterns after a disturbance (Santelices 1990). Reproductive patterns in fucoids are variable, with some being fertile year-round having large pulses in particular months (e.g. *H. banksii*) while others have restricted seasonal reproductive periods (e.g. *C. torulosa*) (Taylor & Schiel 2003, Schiel & Foster 2006).

The relationship between coralline turf and macroalgae has not been extensively investigated (Taylor & Schiel 2005). Both facilitation and inhibition have been shown experimentally (Connell 2003). The balance of this relationship depends on the stage of development of a coralline patch, the nature of sedimentation and the abilities of fucoid and laminarian algae to settle in them. Turfing algae can facilitate the recruitment of fucoid embryos of some species (Brawley & Johnson 1991), but inhibit others (Dayton et al. 1984, Kennelly 1987, Camus 1994). Mechanisms by which either can occur include the provision of suitable microhabitat conditions (Brawley & Johnson 1991, Benedetti-Cecchi & Cinelli 1992), or inhibition by turf shedding their ephelial cells, thus removing recruits settled on them (Camus 1994). This difference in effect may be due to different methods of assessment. Benedetti-Cecchi and Cinelli (1992) found that turfs enhanced embryo settlement, but saw the opposite effect in recruitment as plants grew larger. Clearly post-settlement mortality plays an important role in determining the effects of turfing communities on other species. Turfing communities may increase settlement compared to bare space by providing a refuge from

zygotes getting displaced by wave action (Brawley & Johnson 1991) and grazers (Branch 1981) or by preventing desiccation (Lilley 2004). The amelioration of harsh physical conditions by turfing species may increase as an intertidal site becomes more stressful (Bertness & Leonard 1997). For example, if sedimentation increases, turfing algae may play a facilitative role in fucoid recruitment, preventing abrasion of zygotes (Airoldi 2003).

1.2. Study Aims

This thesis uses field-based experimental manipulations and complementary laboratory experiments to test the relationships between algal turfing communities, sedimentation and habitat-dominating fucoid algae, especially during their early life history stages. I focus on two fucoids, *C. torulosa* and *H. banksii*, the dominant algae on moderately exposed southern New Zealand coasts, and *Corallina officianalis* the dominant understory alga. Overall, I test the hypothesis that the interactive of sediment and coralline algae has significant effects on algal assemblages through settlement and subsequent recruitment processes. In Chapter 2, I quantify the sedimentation regime over temporal and spatial scales around the Kaikoura peninsula, and experimentally test long-term successional change in intertidal communities across a gradient of sedimentation and disturbance. Chapter 3 examines the effect of different types and volumes of sediment on the attachment of fucoid zygotes under laboratory conditions, and how experimentally settled fucoid germlings surived in different sediment and turf environments. Because any anthropogenicically derived increase in sedimentation is likely to be associated with an increase in nutrient levels, especially Nitrogen from agricultural run-off, I examine in Chapter 4 the effects of nutrient addition on algal abundance over a sediment and disturbance gradient.

1.3. Study Sites

Field sites used in this study are located along the eastern coast of the South Island of New Zealand, around the Kaikoura peninsula (Fig 1.1; 42° 25' S, 173° 44' E). The peninsula projects 4 km out to sea, and reaches widths of 1.2 km (McClay 1995). It has large algal-dominated intertidal platforms composed of sedimentary rocks such as sandstone, limestone and calcareous mudstone ranging from Late Cretaceous to the Cenozoic (Rattenbury et al. 2006). Sedimentary rocks are soft and easily eroded (Stephenson & Kirk 1998, Rattenbury et al. 2006), and erosion rates on the Kaikoura peninsula estimated at 1.13mm per year (Stephenson & Kirk 1998). Wind patterns show seasonal trends with southerlies dominating

in winter and northeasterlies in summer (Rasmussen 1965). Although there is strong wave action and swells resulting from the wind, many of the intertidal platforms around the peninsula are sheltered by rocky outcrops and their aspect. Average monthly water temperatures range from 9-18°C (Chiswell & Schiel 2001). The continental shelf is only 4-5 km offshore, and depths of over 2300m occur approximately 20 km southeast of the Peninsula, at the northern end of the Kaikoura canyon (Rasmussen 1965). The Kaikoura canyon acts as a sink for the more than 40 million tonnes of sediment per year discharged along the eastern coast of the South Island from the rising Southern Alps (Griffiths & Glasby 1985). Terrigenous sediments reaching the intertidal platforms are sourced from several rivers located to the north and south of the Peninsula which contribute significant amounts of sediment, especially during flooding. These include the Kowhai and Kahutara rivers to the south and Lyell creek and Hapuka river to the north. Floods have been a part of the history of Kaikoura for as long as records have been kept (ECan 2007), with two such events occurring during 2008.

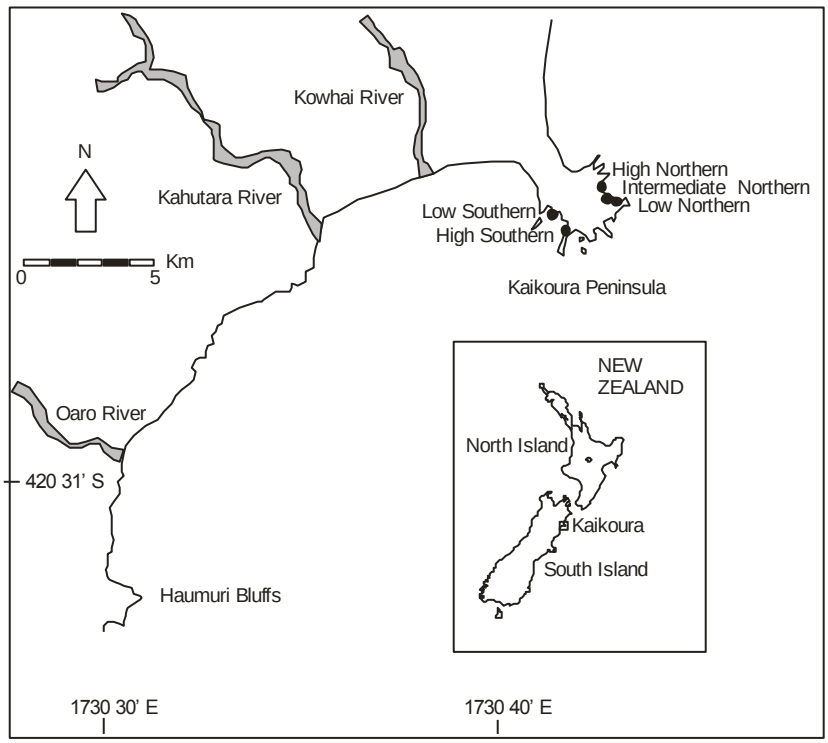


Figure 1.1 Map of study area showing location of study sties used in chapter 2 (High intermediate and low northern and high and low southern), location of experiment in chapter 4 (high southern), and locations of major sediment contributing rivers. Inset showing location of the Kaikoura peninsula.

1.4. Study Species

1.4.1 *Hormosira banksii*

Hormosira Banksii (Turner) Descaisne (Fig 1.2) is a fucoid alga that dominates the mid intertidal zone at many rocky intertidal sites around New Zealand (Schiel 2006) and Australia (Underwood 1998). Buoyant strings of beads form dense clumps in which it is difficult to distinguish individual plants, which can reach ca. 40cm length (Schiel 2006). Reproduction is by antheridia and oogonia produced in sunken conceptacles on the beads, opening to the surface by a conspicuous ostiole. *H. banksii* is dioecious, with sexes recognisable by the colour of mucilage from the ostiole: males orange and females light green (Adams 1994).

1.4.2 *Cystophora torulosa*

C. torulosa (R. Brown) J. Agardh (Fig 1.3) is the dominant fucoid alga in the low intertidal zone (ca 0.2-0.5m above LAT) where it forms a thick, closed canopy. It also occurs as an understory species at the base of the *Hormosira* zone. It has buoyant, multi-branched fronds reaching up to 80cm in length (Schiel 2006). Reproduction is by monoecious and bisexual conceptacles, sunken and opening by ostioles usually in 2 obvious rows on the receptacle (Adams 1994).

1.4.3 *Corallina officianalis*

C. officianalis Linnaeus (Fig 1.4) is the dominant understory turfing alga on the Kaikoura peninsula, and around much of New Zealand (Adams 1994). It is a red, calcareous geniculate alga. Plants are 1-4cm high (Adams 1994) with side branches arranged pinnately on primary stems (Adams 1994). The morphology of the turf is influenced by the sediment environment and, in some places sediment is considered a structural constituent of the turf (Stewart 1989, Kendrick 1991, Airoldi 1998). *C. officianalis* is dioecious with carpospores, spermatangia and tetrasporangia in conceptacles (Adams 1994).

Figure 1.2 *Hormosira banksii* showing characteristic buoyant beads**.**

Figure 1.3 *Cystophora torulosa* with, multi-branched fronds.

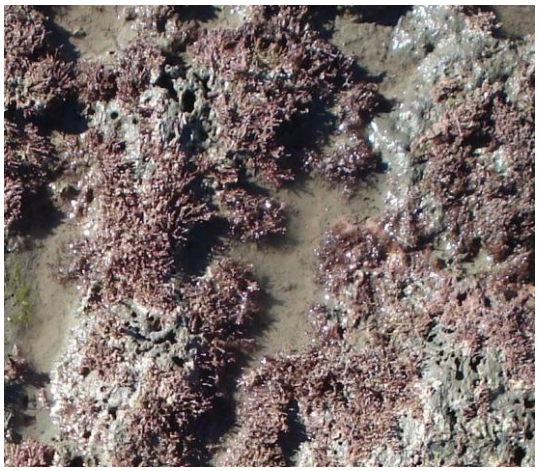
a)  b) 

Figure 1.4 *Corallina officianalis* a) with sediment b) without sediment for experiments from Chapter 2.

Chapter 2. Alteration of the sediment environment: the interactive effects of disturbance

2.1. Introduction

An understanding of how sediment interacts with turfing algae and habitat dominating algae is needed to understand the effects any future increase in sedimentation could have on rocky intertidal organisms (Schiel et al. 2006). Canopy forming algae can ameliorate the harsh abiotic conditions of the intertidal zone by creating a positive interaction and allowing an understory community to be maintained, (Bertness et al. 1999). Canopy-forming algae, however can also prevent understory algae from persisting beneath a canopy through competitive processes (Irving et al. 2004). Whatever process is operating in a community, the loss of canopy-forming species can trigger large changes in benthic communities (Reed & Foster 1984, Santelices & Ojeda 1984).

There are many species of turfing algae, but the dominant one around the Kaikoura peninsula is *Corallina officinalis* (Lilley 2004, Lilley & Schiel 2006, Schiel 2006). The complex branched morphology of this turf causes sediment to be trapped within the branches; indeed, sediment is intrinsic to such a degree it is considered to be a structural constituent of the turf (Stewart 1983, Kendrick 1991, Airoldi & Virgilio 1998).

To investigate the effects of sedimentation on community structure, it is necessary to quantify the sediment environment that affects assemblages (Airoldi 2003). Careful measurements of spatial and temporal variation in the rates of sediment flux and deposition are important in understanding the distribution and abundance of species in different sediment environments (Airoldi et al. 1996). Sediment traps, despite methodological uncertainties (reviewed in Airoldi et al. 1996, Schiel et al. 2006) have been successfully used to quantify the sediment environment in shallow rocky subtidal areas (Airoldi et al. 1996, Airoldi & Virgilio 1998). Several issues arise when measuring the sediment flux in the intertidal zone and across exposure gradients (Schiel et al. 2006): as water flow increases, the efficiency of sediment traps is modified due to the loss of finer particles or because the ability of traps to capture particular size classes is altered (Butman 1986, Butman et al. 1986). On the benthos, the sediment environment in algal turf can be different from the sediment flux. Therefore, measures should be taken to measure the benthic sediment environment (i.e., sediment in the turf), in and on which communities develop, as well as measuring the sediment flux in the

water above reefs (Airoldi & Virgilio 1998). Benthic sediments can be described in terms of depth, percentage cover, weight per unit area and size composition (Airoldi 2003).

Many studies have examined species' distributions across sediment gradients (Daly & Mathieson 1977) without examining causative mechanisms that influence community composition (Airoldi & Cinelli 1997). Field-based experiments seeking to test how the sediment environment affects rocky shore community structure have been done predominantly in the shallow subtidal zone (Airoldi 2003). Studies in the Mediterranean Sea show that small-scale spatial variability in sediment deposition influences within-habitat diversity by altering the abundance of dominant species (Airoldi & Cinelli 1997). Caution needs to be taken when extrapolating these results to other subtidal sites, let alone intertidal habitats, as sediments have different effects on assemblages due to differences in intensity, spatial and temporal patterns of disturbance, particle size, life history and tolerances of the species involved (Airoldi 2003) and increased wave effects in the intertidal zone (Gaylord 1999).

Disturbance, whether from natural or anthropogenic causes, is the primary mechanism for creating bare space in the marine environment, allowing community shifts to occur by influencing the expansion and recruitment of species (Sousa 1984). Patterns of recruitment after a disturbance can be affected by numerous biotic and abiotic interactions. For example, re-colonisation of disturbed areas in the shallow subtidal zone of the Mediterranean Sea depended on the timing, intensity and size of disturbances, and on stress induced by local deposition of sediment (Airoldi 1998). Anthropogenic disturbances can interact with background ecological processes on a range of spatial and time scales, altering relative abundances and community composition (Benedetti-Cecchi et al. 2001). Anthropogenic disturbances such as an increase in sedimentation may override topographical complexity, which is a proposed mechanism for maintaining beta diversity (i.e., variations in the composition and abundance of species among sites) in communities (Balata et al. 2007a).

This chapter presents the results of a thirteen-month long intertidal experiment testing community response to variations in the sediment environment and disturbance in the turfing communities, with a focus on canopy-forming fucoid algae. During this period, benthic sediment and sediment flux were measured in conjunction with experimental manipulations of the algal and turfing community. These manipulations mimicked disturbances, creating bare space in an otherwise space-limited environment (Sousa 1984), or more subtle

disturbances of the environment, particularly a reduction in turf biomass (cf., Airoldi & Virgilio 1998).

2.2. Methods

2.2.1 Experimental Sites

These experiments were done on the Kaikoura peninsula on the east coast of New Zealand's South Island. All experiments were done within stands the dominant algae *Hormosira banksii* in the mid-intertidal zone. Sites were selected to reflect a gradient of sedimentation, based on wave exposure and amount of accumulated sediment. Five sites were chosen across two locations on the northern and southern sides of the peninsula. On the northern side, experiments were established in three sites with "low", "intermediate" and "high" predicted sediment regimes. On the southern side experiments were established at two sites ("high" and "low") due to the lack of a suitable "intermediate" site. The site labels used throughout this chapter reflect location (northern or southern) and predicted levels of sedimentation (high, intermediate and low) based on *a prior* assessment of sediment levels. Four experimental sites were established in November 2007, and the fifth (high northern), in May 2008.

2.2.2 Sediment Traps

To measure the flux in sedimentation at each site, sediment traps were designed to approximate the volume and composition of sediment arriving. 600mL plastic bottles, with an aspect ratio of 2 and internal diameter of 60mm, were used as the collection vessel. A 6mm hole was drilled through the bottom to accommodate a bolt. Two circles of PVC foam (4mm thick) (trade name *sun board, easiroll*), one between the trap and the rock substrate and one inside the container, were used to maintain a tight seal between the rock and the trap. Inside the container were two 10 by 10cm squares of shade cloth, which slowed water flow and trapped fine particles. The bottles had a screw-on plastic lid into which eleven 5mm holes were drilled (collection area 8.63cm^2); this diameter maximised the sediment that could enter the trap, but minimised the opportunity for re-suspension and loss of fine particles. Three sediment traps were placed at each site using 150mm long stainless steel bolts that were anchored to the rock via 8mm Ramset™ rawl plugs. Bolts were made from 6mm gauge threaded rod onto which two nuts had been welded, so the rod could be screwed to the

substrate via a socket and speed wrench. A third nut was placed 4mm from the base to hold the sun board circles and sediment trap flush to the substrate. Sediment traps were left out for between 3 and 14 days depending on tidal accessibility. Traps were removed and placed into zip lock bags to retain sediment in transit. New, clean traps were used to replace those that had been removed or lost. Traps were frequently lost due to weather and human interference.

At the laboratory, each sediment trap was disassembled and all parts washed thoroughly into a 3L container. The sediment slurry was then passed through a stack of 5 sieves. These were 175mm diameter plastic tubs with nylon mesh of different gauges stretched over an open base; the edges were sealed with silicone to prevent leakage. Mesh gauges were chosen to approximate the Wentworth Grain Classification scale (Chien & Wan 1999). Mesh gauges were 500µm (coarse sand and algal fragments), 250µm (medium sand), 100µm (fine sand), 53µm (coarse silt) and 25µm (medium silt). The samples were sieved over a 25L bucket to collect all particles <25 µm (fine silts). The sediment slurry was gently washed through the sieves, and the material left in each sieve was put into pre-weighed foil containers. The <25 micron fraction was left to settle (6-72 hours), then the water was decanted off and the remaining fine sediments washed into pre-weighted foil containers. The foil containers were placed into a drying oven at 65^{o}C for at least 48 hours. Samples were reweighed and the foil weight subtracted.

2.2.3 Turf samples

To assess the relationship between sediments arriving at sites (using sediment traps) and the benthic sediment environment, 5 coralline turf core samples were taken monthly at each site. These consisted of a 50mm diameter PVC pipe being pushed into the turf/sediment, avoiding other algae as much as possible. The core was then scraped off and placed into a labelled bag. At the laboratory, core samples were mixed with water in a beaker and all coralline turf was removed. The turf was placed into a pre-weighed foil container and 10 random branches were measured, and the entire turf sample was then dried. The sediment washed from the turf was processed in the same way as the sediment trap samples (section 2.2.1).

2.2.4 Long Term Successional Changes

This experiment examined community responses to a manipulation of the sediment regime and disturbance of turfing communities.

At each site, large patches of coralline turf were identified. Eighteen 0.25m^2 quadrats were randomly placed, at least 2m apart to avoid interactions between treatments. Plots were marked with three, 65mm galvanised coach bolts, with a plastic cow tag labelling treatment and replicate in one corner. An initial monitor of species abundances and physical characteristics was done. For algae, sessile invertebrates, bare space and sediment, percent cover was estimated. Mobile invertebrates were counted. Sediment depth was measured and grain size estimated (silt, sand and gravel). Plots were then randomly assigned to one of six treatments (+turf +sediment, +turf –sediment, ½turf +sediment, ½turf –sediment, total clearance and control). In all treatments, except for controls, fucoid species were removed by pinching the algae off at the holdfast after the initial monitor. Fucoids were removed to track recruitment of fucoid juveniles without the effect of canopy.

In –sediment plots, all sediment was removed with a water blaster after the initial monitor. Sediment removal required re-treatment for the duration of the experiment; this was carried out fortnightly using a hand-operated water pump and buckets. Some sediment accumulation did occur, but lowered levels were maintained throughout the experiment. At the high northern site, treatment became impractical between 25 August and 1 October as an extreme weather event caused dramatic alterations to the substratum.

Because sediment load is tightly bound with the depth and cover of coralline turf (Airoldi, 2003) manipulation of turf height was done after fucoids were removed. To do this the understory coralline turf was scrubbed using a wire brush, thereby reducing the turf to approximately half its original height (½ turf). Total clearances were achieved by scraping the plots with metal pry bars, to mimic the effect of extreme disturbance. Sites with more complex topography made scraping difficult and it is likely that some organisms remained deep within cracks. These treatments represent a gradient of disturbance, from +turf +sediment, where only fucoids were removed, through to clearances where all algae were removed. Plots were monitored monthly to record species abundances and physical characteristics.

2.2.5 Data analysis

Experimental data were analysed using analysis of variance (ANOVA) in which sites were treated as a random factor. Prior to ANOVA, Cochran's tests were performed and, where necessary, data were log-transformed to stabilise variances. In some cases variances could not be stabilised through transformation. In these cases the significance level was adjusted to 0.01 to reduce the chance of type I error (Sokal & Rohlf 2003). To establish correlates of the temporal variation in the sediment flux around the Kaikoura peninsula, weather data were obtained from the National Climate database (Cliflow) and regression analysis used. Data for wind strength and direction and rainfall were used from the Kaikoura weather station (42°42' S 173°69'1 E). All analyses were carried out using *Statistica* 7.1.

2.3. Results

2.3.1 Sediment flux

The average daily sediment flux over one year ranged from 37.4g/day at the high northern site to 2.0g/day at the low southern (Fig 2.1). Sediment flux was significantly higher at the high northern site when compared to all other sites (Tukey HSD, $p<0.001$), and significantly lower at the low southern site (Tukey HSD, $p <0.001$). Sites on the same side of the peninsula were different from each other (Tukey HSD, $p<0.05$). Mean daily sediment flux became more variable with increasing sediment flux. The low sites showed less variability over the study period than did the high sites (Fig 2.1). Sites also varied in the composition of the sediment (Fig 2.2). Fine sands (100-250µm) were the dominant size fraction at four sites, making up 74% of total sediment flux at the high northern site, with the low southern site being dominated by fine silts (<25 µm). As mean sediment flux decreased, the composition of the sediment became more uniform.

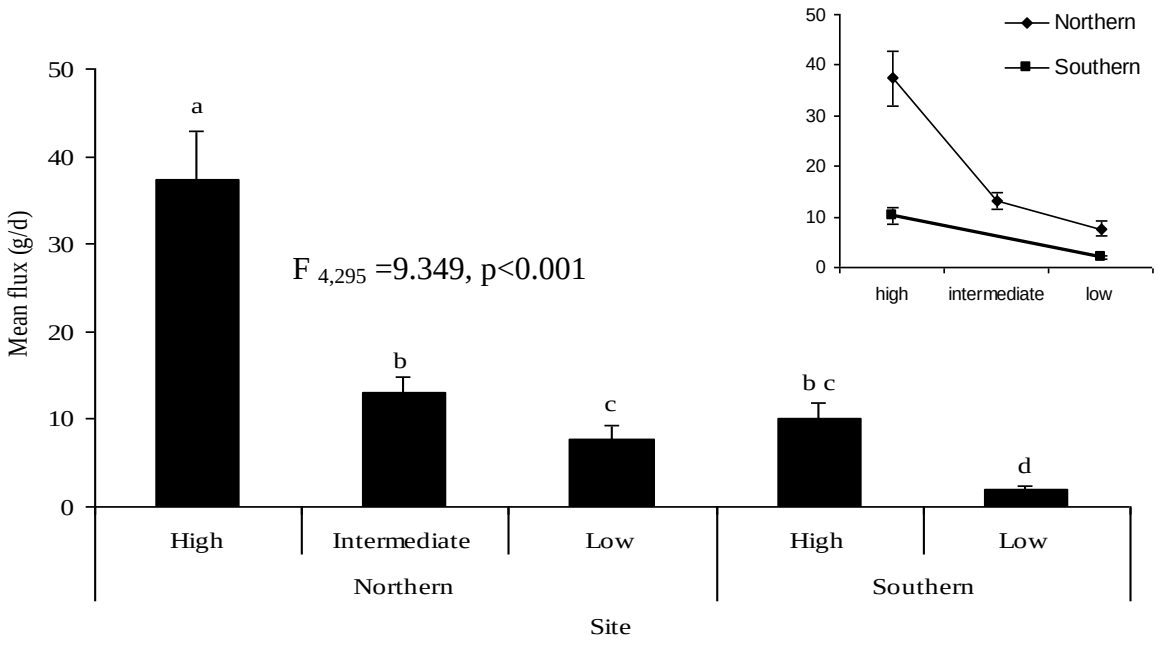


Figure 2.1 Mean daily sediment flux (grams per day) by site, for the period December 2007-November 2008 (+SE). Letters denote homogenous groups (Tukey HSD, p <0.05). Inset data displaced as gradient of the predicted sedimentation at the outset of the experiment.

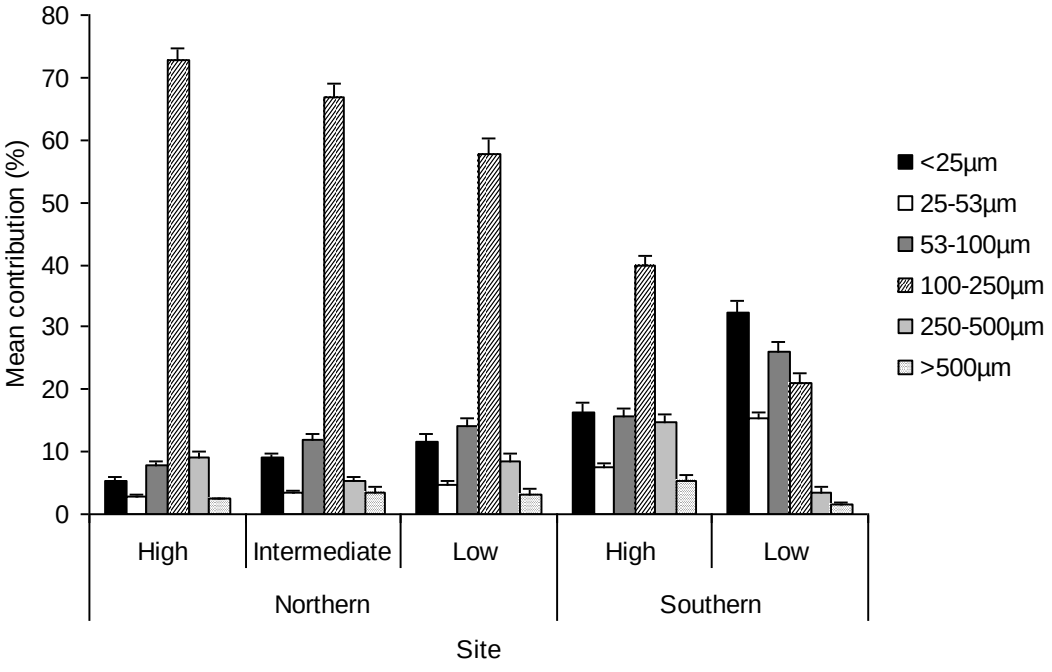


Figure 2.2 The mean percent contribution of size class fractions to sediment flux by site for the period December 2007-November 2008 (+ SE).

There was a significant interaction between site and season when assessing the total sediment flux (Table 2.1). This is due to the significantly higher rate of sediment flux at the high northern site during spring (Fig 2.3) when the maximum sediment flux was 195g/day. During summer the sediment flux was at its lowest and was more consistent between sites

(Tukey HSD, comparisons p>0.415). The >500 µm fraction did not vary significantly between seasons (Table 2.2), but was significantly higher at both the high sediment sites (Tukey HSD, comparisons p<0.010). The 250-100µm fraction was significantly higher at the high northern site from all others in winter autumn and spring (Tukey HSD, p<0.001 all comparisons) (Table 2.2). The >25 µm was significantly higher at both the low southern sites during winter (Tukey HSD, p<0.03) and high southern during spring (Tukey HSD, p<0.001).

Monthly sediment flux had a positive correlation with monthly rainfall (Fig 2.4). There is significantly more sediment at the high northern site than for any other site (Tukey HSD, p<0.003) (Table 2.3). Sediment flux did not correlate with any of the other meteorological variables examined, wind strength (Table 2.4) or wind direction ($F_{2,148}$=2.747 p=0.106).

Table 2.1 Two-way ANOVA on the effects of sites and seasons on the daily sediment flux (grams per day). Summer December – February, autumn March-May, winter June – August, spring September-November. Significance level p<0.01 significant Cochran's.

Effect	df	SS	MS	F	p
Site	4	50162.3	12540.57	9.349	**<0.001**
Season	3	7304.9	2434.98	2.214	0.127
Site*Ssn	12	18908.0	1575.67	4.598	**<0.001**
Error	296	101433.1	342.68		

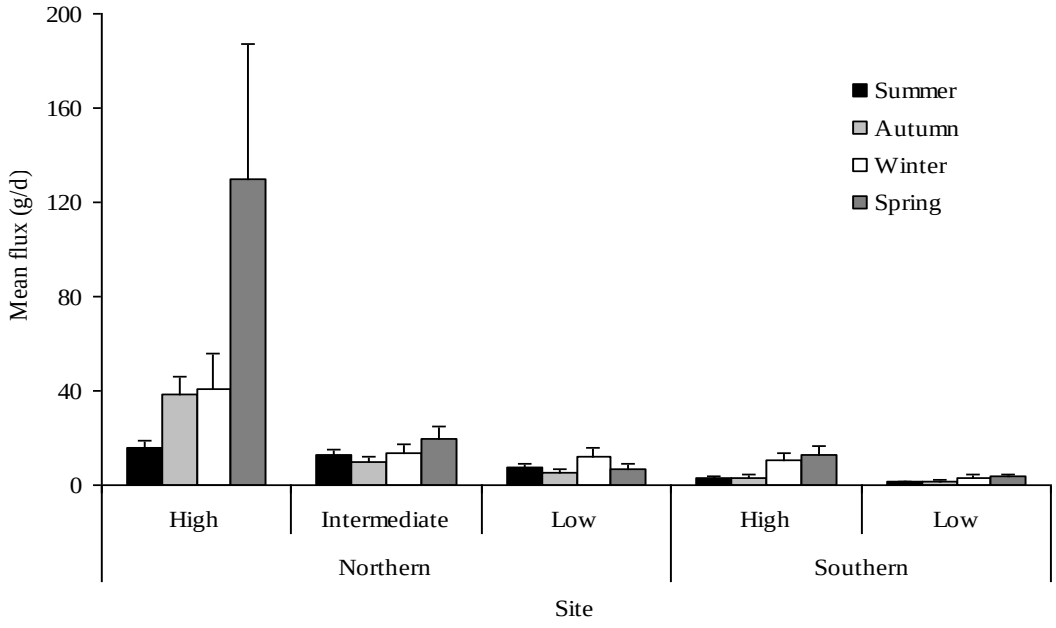


Figure 2.3 Seasonal differences in the mean daily flux (grams per day) by site (+ SE). Summer: December – February, autumn: March-May, winter: June – August, spring: September-November.

Table 2.2 Two-way ANOVA on the effect of sites and test seasons of the flux of size classes (grams per day). Significance level p<0.01 significant Cochran's. a) >500 µm b) 250-100 µm c) >25 µm. Summer December – February, autumn March-May, winter June – August, spring September-November.

Effect	df	SS	MS	F	p
a) >500 µm					
Site	4	13.729	3.432	6.767	**0.002**
Season	3	3.866	1.289	2.886	0.061
Site*Ssn	12	6.791	0.566	2.204	0.012
Error	296	76.007	0.257		
b) 250-100 µm					
Site	4	38664.34	9666.086	7.913	**0.002**
Season	3	4991.43	1663.810	1.689	0.213
Site*Ssn	12	17408.54	1450.712	5.944	**<0.001**
Error	296	72237.02	244.044		
c) >25 µm					
Site	4	3.824	0.956	0.930	0.475
Season	3	10.034	3.344	3.842	0.028
Site*Ssn	12	14.176	1.181	3.138	**<0.001**
Error	296	111.433	0.376		

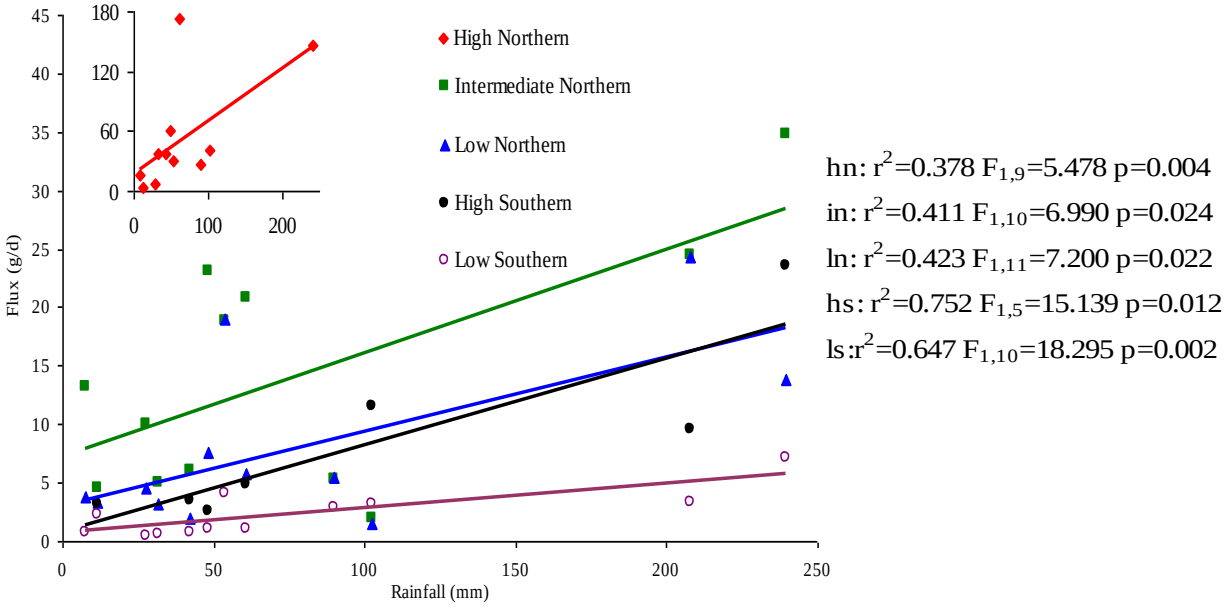


Figure 2.4 Mean monthly sediment flux (grams per day) against mean monthly rainfall (mm). Simple linear regression used to test the relationship between sediment flux and rainfall at each site. Inset high northern site, note larger scale.

Table 2.3 ANCOVA on the variation of the relationship between mean monthly sediment flux (grams per day) and monthly rainfall (mm) between sites.

Effect	df	SS	MS	F	p
Rainfall	1	4812.08	4812.082	8.230	**0.006**
Site	4	19645.74	4911.436	8.410	**<0.001**
Error	48	28032.11	584.002		

Table 2.4 Linear regression of average wind strength for the period of trap deployment (meters per second) and sediment flux (grams per day).

Site	r^2	df	F	p
a) high northern	0.006	1,28	0.156	0.796
b) intermediate northern	0.005	1,38	0.196	0.660
c) low northern	0.041	1, 39	1.667	0.203
d) high southern	0.002	1,18	0.040	0.843
e) low southern	<0.001	1,30	0.020	0.890

2.3.2 Benthic sediment environment

The benthic sediment environment fluctuated between sites across seasons (Table 2.5). The standing mass of sediment was lower at the low northern and southern sites than at all other sites (Tukey HSD, $p<0.005$) (Fig 2.5). There was no relationship between the benthic sediment environment and sediment flux at any of the sites (Fig 2.6). This varied between sites (Table 2.6), with higher values at the high northern site (Tukey HSD, $p <0.007$).

Turf height was significantly different between sites (Table 2.7), being higher at the high and intermediate northern sites (Tukey HSD, $p<0.05$) and lower at the low southern site (Tukey HSD, $p<0.05$) (Fig 2.7). Turf height did not fluctuate significantly between seasons (Table 2.7). There was a positive relationship between turf height and the dry weight of sediment held within the turf ($r^2=0.458$) (Fig 2.8).

Turf biomass was different between sites and season (Table 2.8). Site differences were due to lower biomass at the low northern site compared to all other sites (Tukey HSD, $p<0.001$ comparisons between all sites). Except for the high southern site, turf biomass was generally greatest in autumn and least in spring/summer. Turf biomass had a positive relationship to standing stock of sediment ($r^2= 0.44$) (Fig 2.10).

The percentage contributions of different size fractions were similar between the benthic sediment environment and sediment flux (Fig 2.11). The >500µm fraction contributed proportionality more in the benthic samples than in the sediment flux across all sites (Fig 2.11). At all sites, except for the high northern, the finer sediment fractions (those less than 100 µm) made up a significantly higher proportion in sediment flux (Fig 2.11).

Table 2.5 Two-way ANOVA of the effects of site and season on the standing sediment (kilograms per metre^2). Log transformed data.

Effect	df	SS	MS	F	p
Site	4	56.701	14.175	55.556	**<0.001**
Season	3	1.416	0.472	1.850	0.138
Site* Ssn	12	5.719	0.477	1.868	**0.038**
Error	293	74.759	0.255		

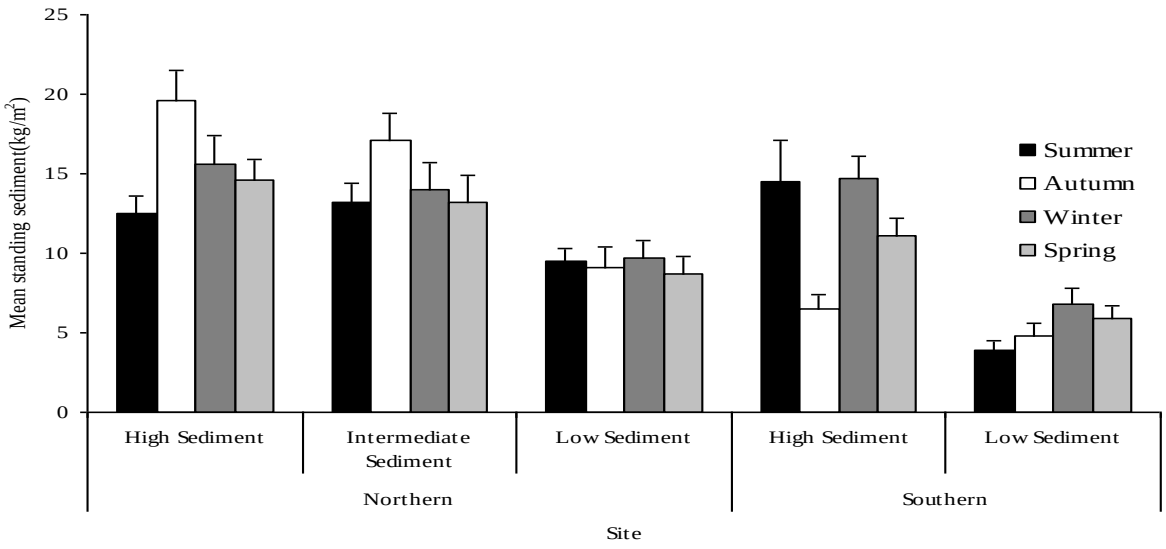


Figure 2.5 Site and seasonal fluctuations in the benthic sediment environment, measured as weight of sediment contained within the turf (+SE). Summer: December – February, autumn: March-May, winter: June – August, spring: September-November.

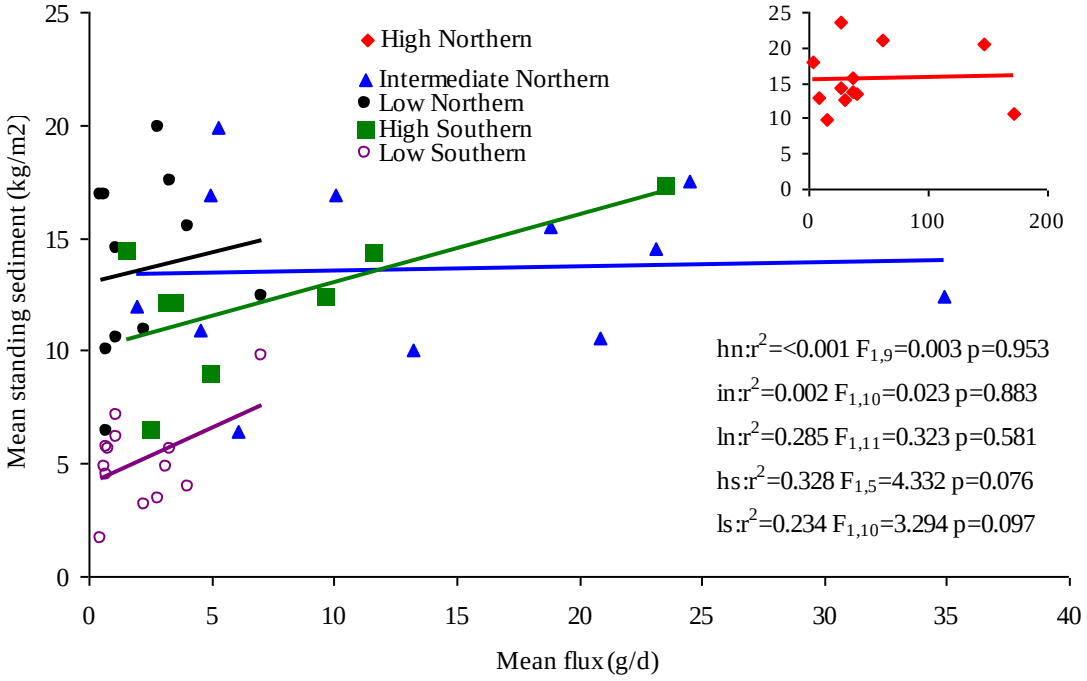


Figure 2.6 Mean sediment flux (grams per day) and against mean standing sediment (kilograms per metre^2). Linear regression used to test the relationship between sediment flux and standing sediment, separate analysis for each site. Insert high northern site.

Table 2.6 ANCOVA on the variation of the relationship between mean monthly sediment flux (grams per day) and standing sediment (kilograms per metre^2) between sites.

Effect	df	SS	MS	F	p
Flux	1	116.26	116.258	0.184	0.670
Site	4	11533.25	2883.312	4.565	**0.003**
Error	52	32845.29	631.640		

Table 2.7 Two-way ANOVA on the effect of site and season on average turf height (mm), based on 10 measurements from each core taken from unmanipulated areas. Significant Cochran's p<0.01. Summer: December – February, autumn: March-May, winter June – August, spring: September-November.

Effect	df	SS	MS	F	p
Site	4	1083.19	270.80	43.635	**<0.001**
Season	3	31.74	10.58	1.705	0.166
Site* Ssn	12	154.15	128.5	2.070	0.019
Error	291	1805.92	6.21		

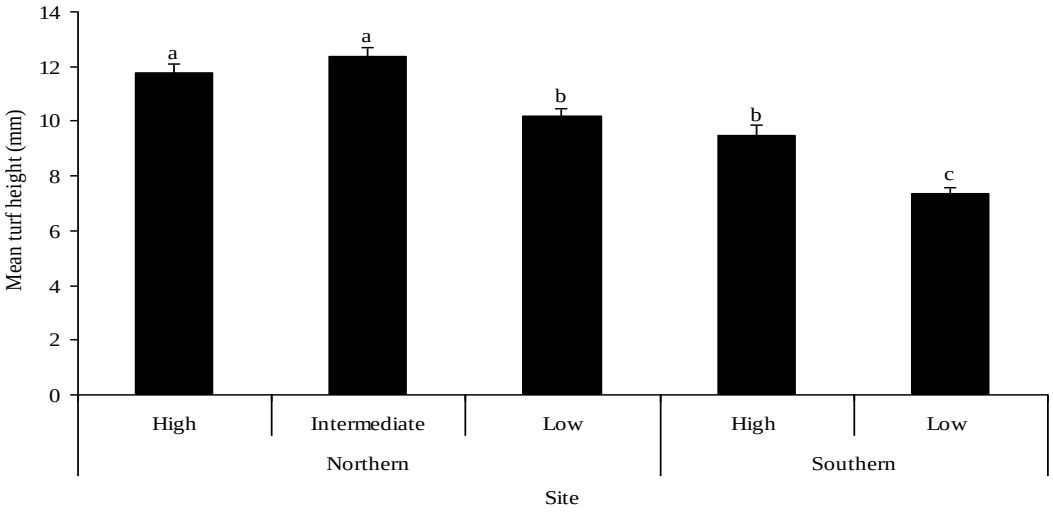


Figure 2.7 Variation in mean turf height (mm) (+SE) between sites. Values obtained from 10 random measurements per core data pooled from November 2007-December 2008, from unmanipulated areas. Letters denote homogenous groups, Tukey HSD, p = 0.1.

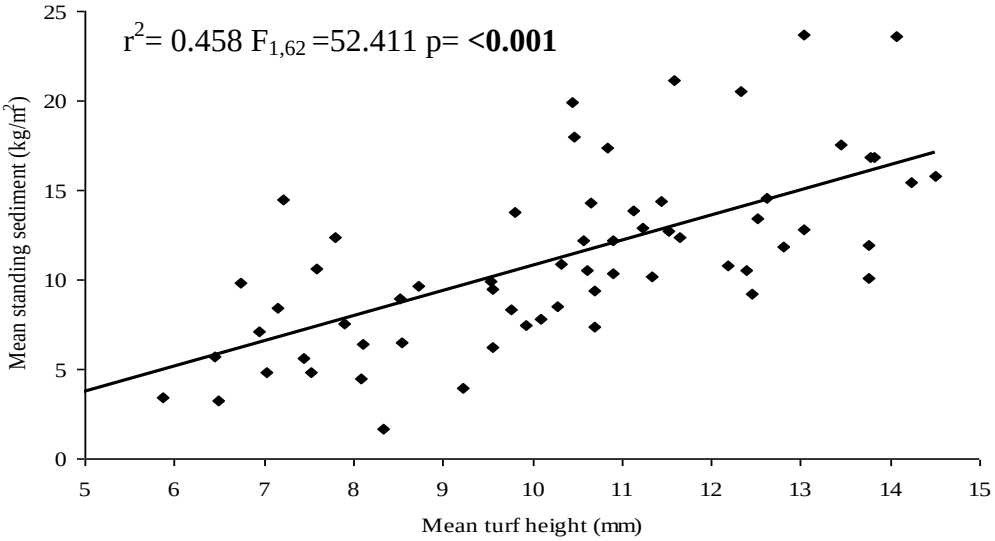


Figure 2.8 Mean standing sediment (kilograms per meter^2) against mean turf height (mm). Linear regression was used to test the relationship between standing sediment and turf height.

Table 2.8 Two-way ANOVA on the effect of site and season on turf biomass standardised to kilograms per m^2). Significant Cochran's p<0.01. Summer: December – February, autumn: March-May, winter June – August, spring: September-November.

Effect	df	SS	MS	F	p
Site	4	106.281	26.570	32.270	**<0.001**
Season	3	20.328	6.774	8.227	**<0.001**
Site* Ssn	12	19.687	1.641	1.993	**0.023**
Error	293	241.249	0.823		

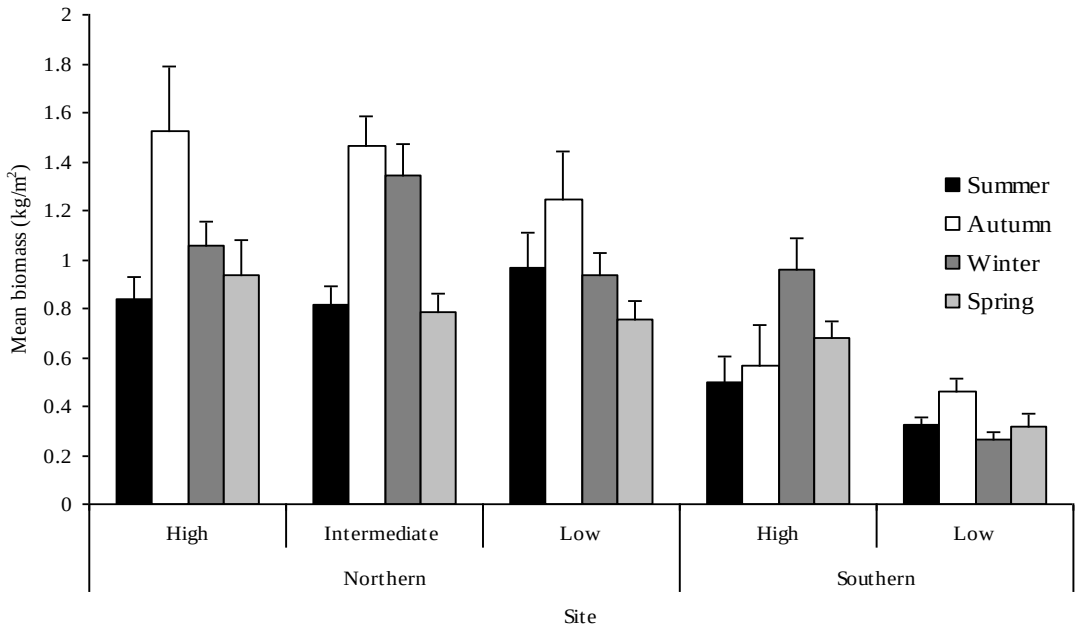


Figure 2.9 Site and seasonal differences in mean turf biomass (kilograms per $metre^2$) (+SE). Seasons: Summer: December – February, autumn: March-May, winter: June – August, spring: September-November.

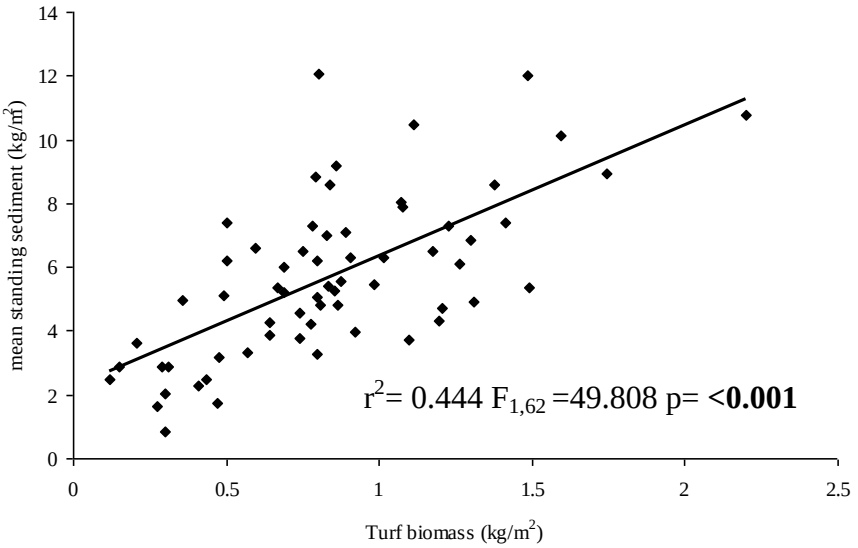


Figure 2.10 Mean standing sediment (kilograms per $metre^2$) and against mean turf biomass (kilograms per $metre^2$). Simple linear regression used to test the relationship between standing sediment and turf biomass, separate analysis for each site.

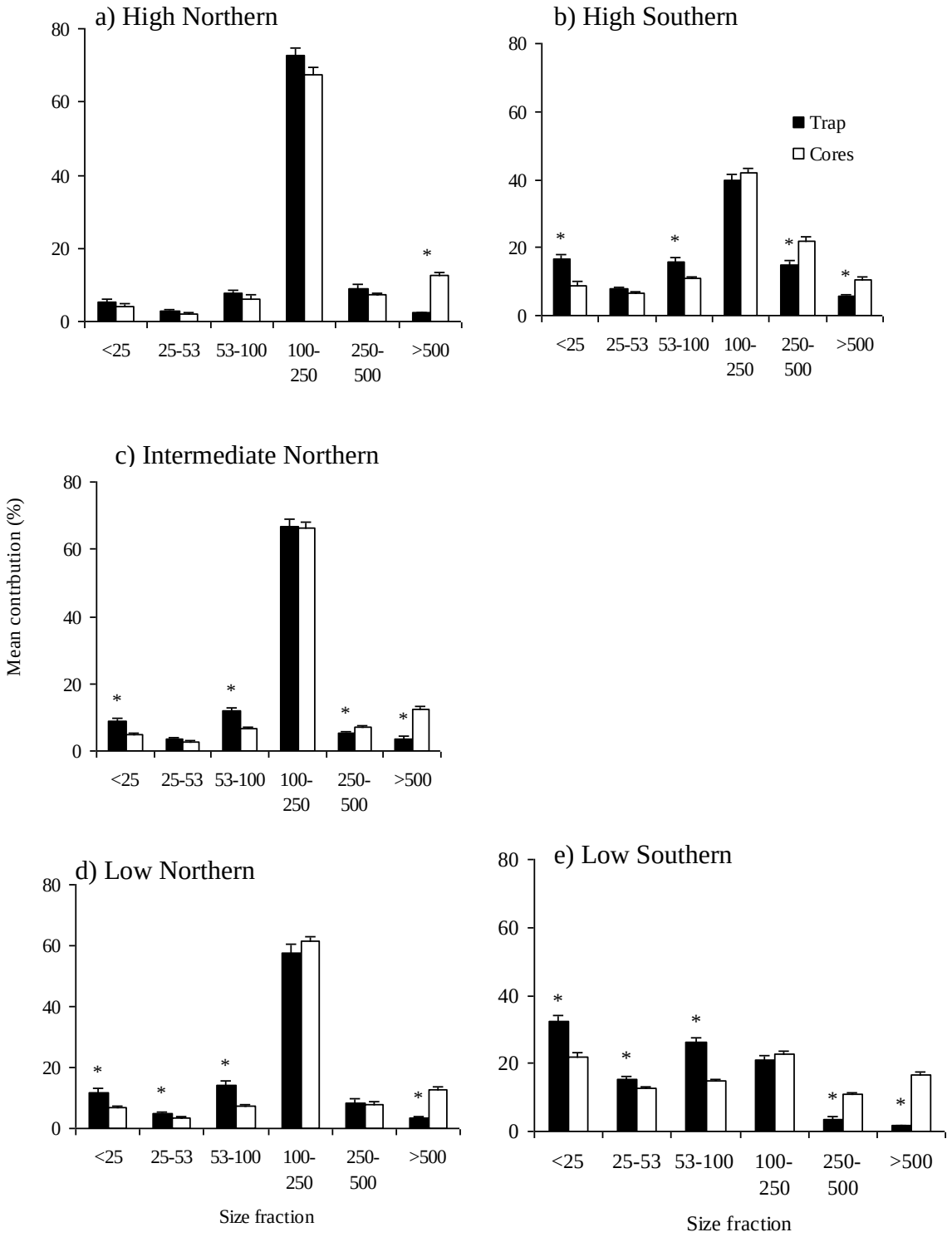


Figure 2.11 Mean percentage contribution of different size classes (+SE) in sediment flux (filled bars) and core samples (open bars). Asterisk denote significant differences ANOVA $p<0.05$. a) high northern b) intermediate northern c) low northern d) high southern e) low southern.

2.3.3 Long term succession experiment

Averaged over the 13 month experiment, algal diversity varied by site and treatment (Table 2.9). The highest diversity was found at the intermediate northern site, and lowest at the high northern (Fig 2.12). Differences in diversity between treatments were not consistent between sites: the intermediate northern site had significantly higher diversity in the +turf -sediment treatment clearance and the ½ turf treatments (Tukey HSD, p=<0.001) and the low southern had lower diversity in the clearance treatment compared to the control treatments (Tukey HSD, p=0.002) other sites had no significant differences between treatments.

Table 2.9 Two-way ANOVA on algal diversity between sites and treatments diversity across the entire study period (December 2007-December 2008).

Effect	df	SS	MS	F	p
Site	4	643.167	160.7918	14.31153	**0.001**
Treatment	5	185.519	37.1038	3.40225	**0.021**
Site*treatment	20	224.705	11.2353	3.69912	**<0.001**
Error	1120	3401.755	3.0373		

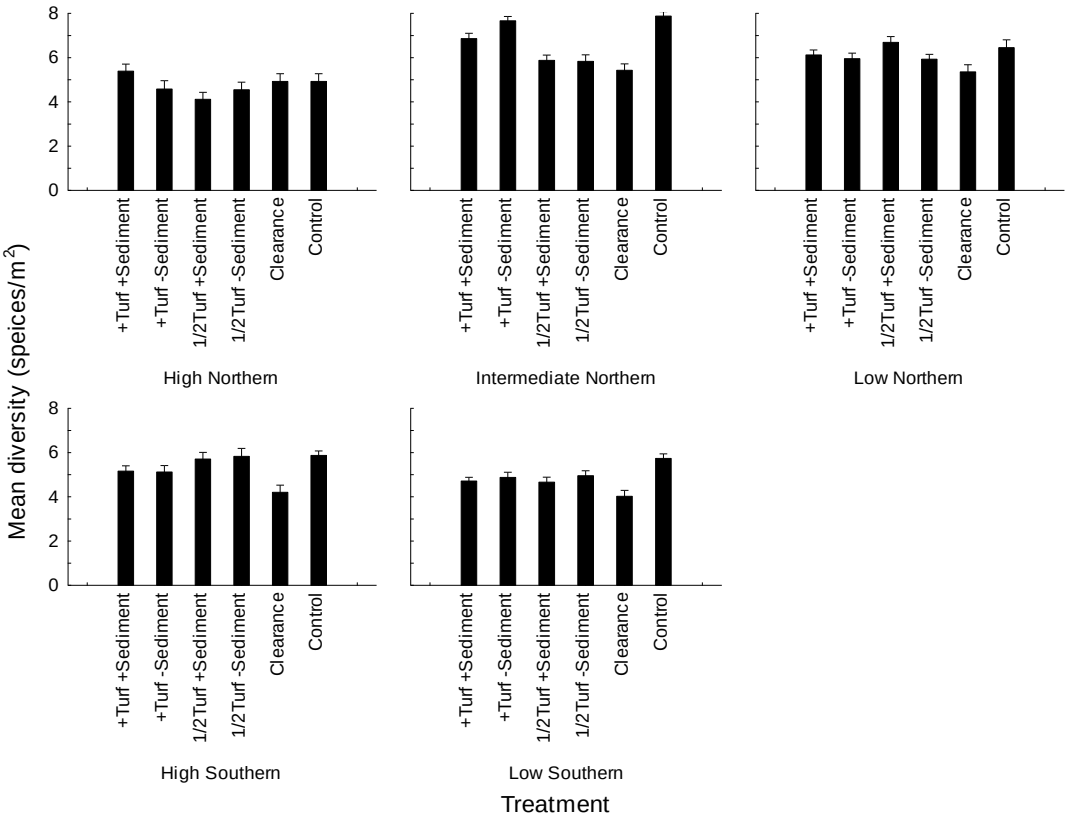


Figure 2.12 Variation in mean (+SE) standing algal diversity between sites and treatments across the study period (December 2007-2008).

2.3.3.1. Understory algae

Green algae showed the greatest response to experimental treatments. They recruited particularly well to complete clearances of turf and sediment, but with significant interactive effects through time (Fig 2.13). The dominant green algae were the ephemeral *Ulva* spp.. After only one month post-manipulation they were significantly different among sites (Table 2.10 a), with the greatest cover of 29% at the high northern clearance treatments. After six months, there was a site x treatment interaction (Table 2.10 b), with the clearance treatments at the low southern site having 91% cover. After twelve months, sites and treatments were significantly different but not their interaction (Table 2.10 c). All sites except high northern had the greatest covering in clearance treatments, but the magnitude varied from 35% at the low southern site to 0.5% at the low northern. The low southern site had the largest response of green algae; after four months the cover in the cleared treatment was 100%. This high cover was maintained for three months before a die-off to 40-50% cover. The high southern site also had a significant ephemeral response with cover of *Ulva* spp. increasing until five months after treatment application followed by a rapid die off over one month to virtually nothing by December 2009 (Fig 2.13). On the northern side of the peninsula there was no response of green algae at the low and intermediate sites associated with the disturbance of the turfing community. There was only a slight peak at the low northern site after 14 months. Green algae at the high northern site showed two distinct peaks in percent cover during January 2008 and December 2008. The response was highly variable within treatments, with one of the clearance replicates reaching 96% cover and the two others with less than 5% cover. On the southern side of the peninsula, ephemeral green algae showed a response along the gradient of disturbance with highest covering in clearances followed by the ½turf – sediment through to +turf +sediment where only fucoids were removed.

Brown algae (non-fucoid) occurred predominantly on the northern side of the peninsula (Fig 2.14). After one month there was a significant site x treatment interaction (Table 2.11 a) with the greatest covering of 22% in the control treatment at the low southern site. The effect of site on non-fucoid brown algae interacted with treatments after six months (Table 2.11 b) with peaks in abundance at the high northern site across all treatments (Fig 2.14). There were no significant site or treatment differences after 12 months (Table 2.11 c). The majority of non-fucoid brown algae were ephemeral and reached maximum abundance in early spring. Species dominating these blooms were *Colpomenia spp*. (Scytosiphonales), *Adenocystis utricularis* (Scytothamnaceae) and *Scytosiphon lomentaria* (Scytosiphonales).

These were generally absent from the southern side of the peninsula (Fig 2.14). At the high northern site, the total clearance treatment had the largest response, mainly due to a high covering of *Colpomenia* spp.. The low northern site showed a peak in abundance of brown algae eight months after treatment application (September 2008) across all treatments, but the magnitude of the response was greater in the +turf +sediment treatments (Fig 2.14).

The main response of filamentous red algae was on the southern side of the peninsula (Fig 2.15). There was a significant interaction between sites and treatments in the response of red filamentous algae at one month (Table 2.12 a), with reduced cover in all treatments at the high northern site (Fig 2.15). Significant site and time interactions were also seen at six months after treatment application, (Table 2.12 b), with highest percentage cover at the high southern site, which was up to 60% covering in the total clearances. Differences between treatments at the high southern site were evident at 12 months; the seasonal peak in coverage observed in the control treatments was not replicated in the total clearances and ½turf – sediment treatments. At the low southern site, the total clearances did not have the first of the seasonal peaks in abundance at 5 months. There were not only differences in the abundance of red filamentous algae between sites but also in species composition. The most abundant alga on the southern side of the peninsula was *Polysiphonia decipiens* (Rhodomelaceae), but the northern side was dominated by *Ceramium* spp. (Ceramiales).

Turfing and encrusting red algae also showed significant site and treatment differences, at one (Table 2.13a) and six (Table 2.13b) months after treatment application. The fluctuation between treatments and sites was explained by the variation in *Corallina officinalis* cover. These were expected because of initial treatment application. However, after 13 months there was limited recovery in total clearance treatments, with highest recovery at the high northern site at 31% cover (Fig 2.16). In the treatments where the turf height was reduced, there was also an associated reduction in percent cover of those turfs. The magnitude of this reduction varied between sites (Fig 2.16). At the intermediate northern site there was a dramatic reduction after two months, especially where sediment removal also occurred, and recovery began 10 months after treatment application. Reduction in percentage cover associated with reductions in turf height occurred also at the low southern site but not to the same extent. Significant fluctuations in turfing algae cover at the remaining sites across all treatments obscured any reductions in cover due to ½ turf treatments.

Table 2.10 Two-way ANOVA on the effect of treatment and sites on the percentage cover of green algae a) 1 month after treatment application b) 6 months after treatment application and c) 12 months after treatment application.

Effect	df	SS	MS	F	p
a)Site	4	1208.949	302.237	4.898	**0.006**
Treatment	5	310.123	62.026	1.005	0.440
S*T	20	1234.064	61.703	1.361	0.179
Error	60	2720.173	45.336		
b)Site	4	614970	1537.426	1.899	0.150
Treatment	5	12951.93	2590.386	3.203	**0.028**
S*T	20	16257.01	812.851	6.336	**<0.001**
Error	58	7441.21	128.297		
c)Site	3	814.042	271.342	3.680	**0.036**
Treatment	5	1591.146	318.230	4.3157	**0.012**
S*T	15	1106.068	73.739	0.452	0.953
Error	48	7836.313	163.257		

Table 2.11 Two-way ANOVA on the effect of treatment and sites on the percentage cover of understory brown algae a) 1 month after treatment application b) 6 months after treatment application and c) 12 months after treatment application.

Effect	df	SS	MS	F	p
a) Site	4	416.170	104.073	2.025	0.130
Treatment	5	624.458	124.892	2.430	**0.071**
S*T	20	1027.715	51.386	2.038	**0.018**
Error	60	1512.940	25.216		
b) Site	4	17.427	4.358	1.585	0.217
Treatment	5	36.163	7.233	2.634	0.055
S*T	20	55.130	2.757	2.749	**0.001**
Error	58	58.167	1.003		
c) Site	3	31.953	10.659	1.900	0.173
Treatment	5	17.725	3.545	0.632	0.678
S*T	15	84.105	5.607	0.938	0.531
Error	48	286.867	5.976		

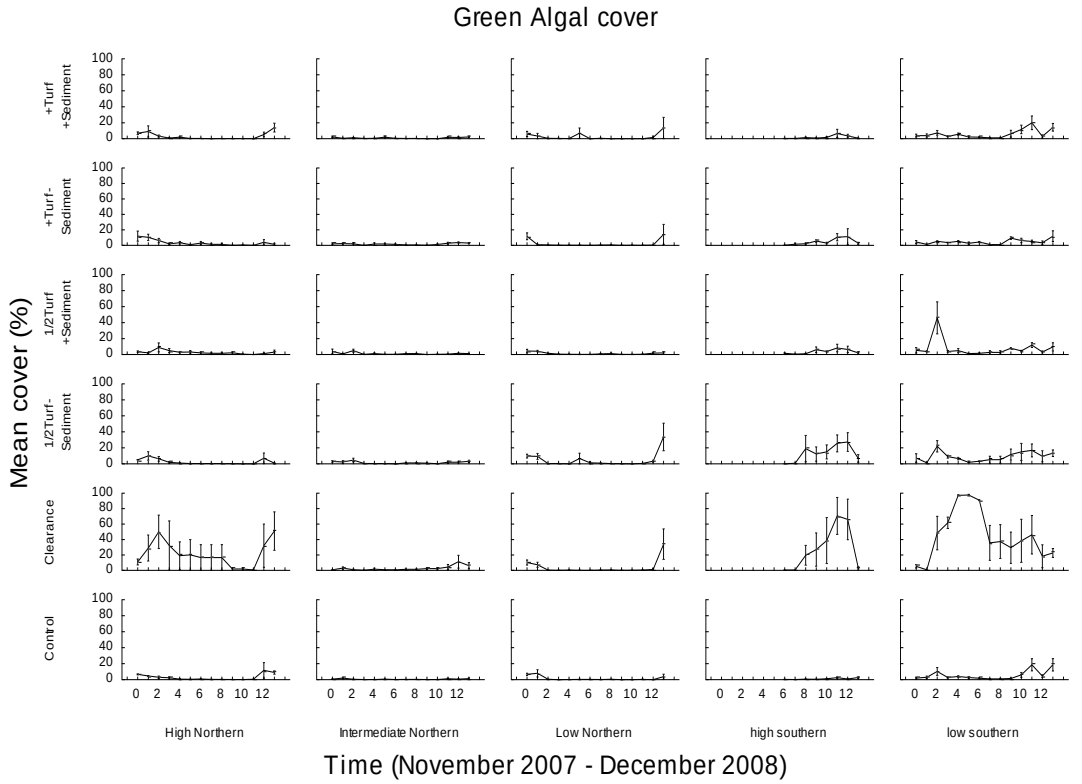


Figure 2.13 Temporal variation in the mean (±SE) percent cover of green algae between sites and treatments. Time measured in months 0=November 2007 through to 14=December 2008.

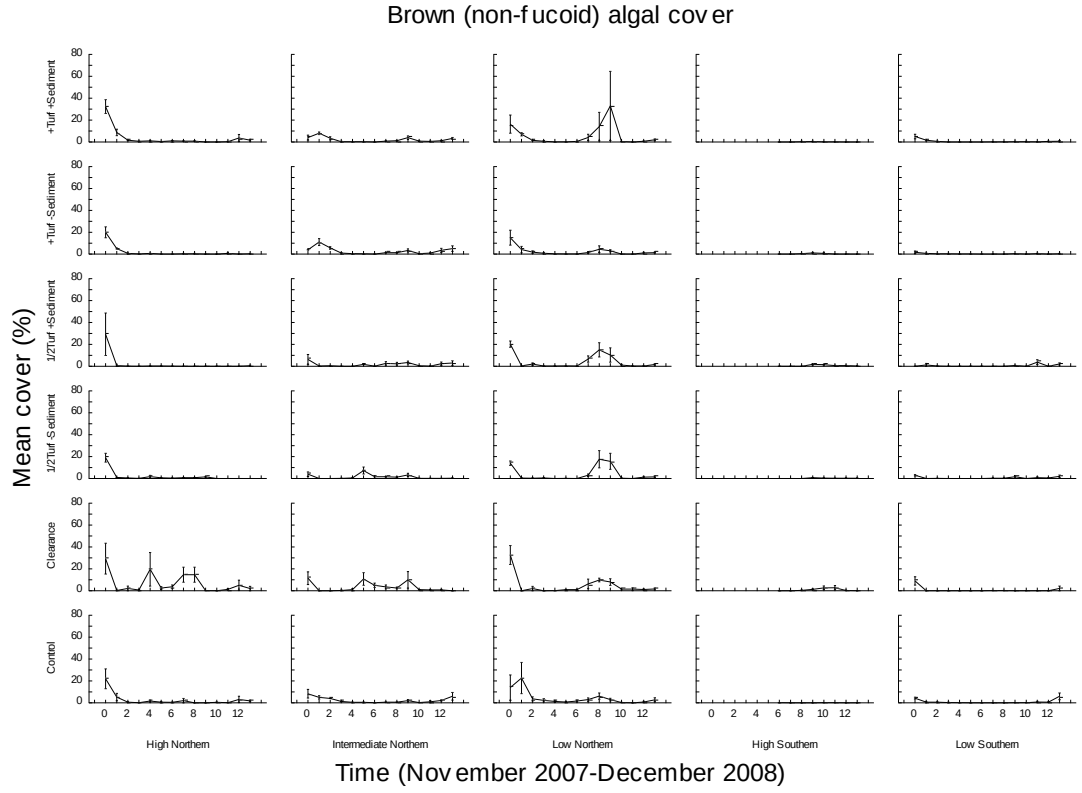


Figure 2.14 Temporal variation in the mean (±SE) percent cover of understory brown algae between sites and treatments. Time measured in months 0=November 2007 through to 14=December 2008.

Table 2.12 Two-way ANOVA on the effect of treatment and sites on the percentage cover of red filamentous algae a) 1 month after treatment application b) 6 months after treatment application and c) 12 months after treatment application.

Effect	df	SS	MS	F	p
a) 1 Months after treatment application					
Site	4	557.568	139.392	9.124	**<0.001**
Treatment	5	151.821	30.364	1.987	0.287
S*T	20	305.556	15.278	1.076	**<0.001**
Error	60	851.633	14.194		
b) 6 Months after treatment application					
Site	4	35721.12	8930.279	11.560	**<0.001**
Treatment	5	5184.39	1036.879	1.343	0.287
S*T	20	15500.47	775.024	3.230	**<0.001**
Error	58	13916.30	239.936		
c) 12 Months after treatment application					
Site	3	12.020	4.007	3.059	0.060
Treatment	5	4.404	0.881	0.672	0.650
S*T	15	19.645	1.310	0.732	0.740
Error	48	85.853	1.789		

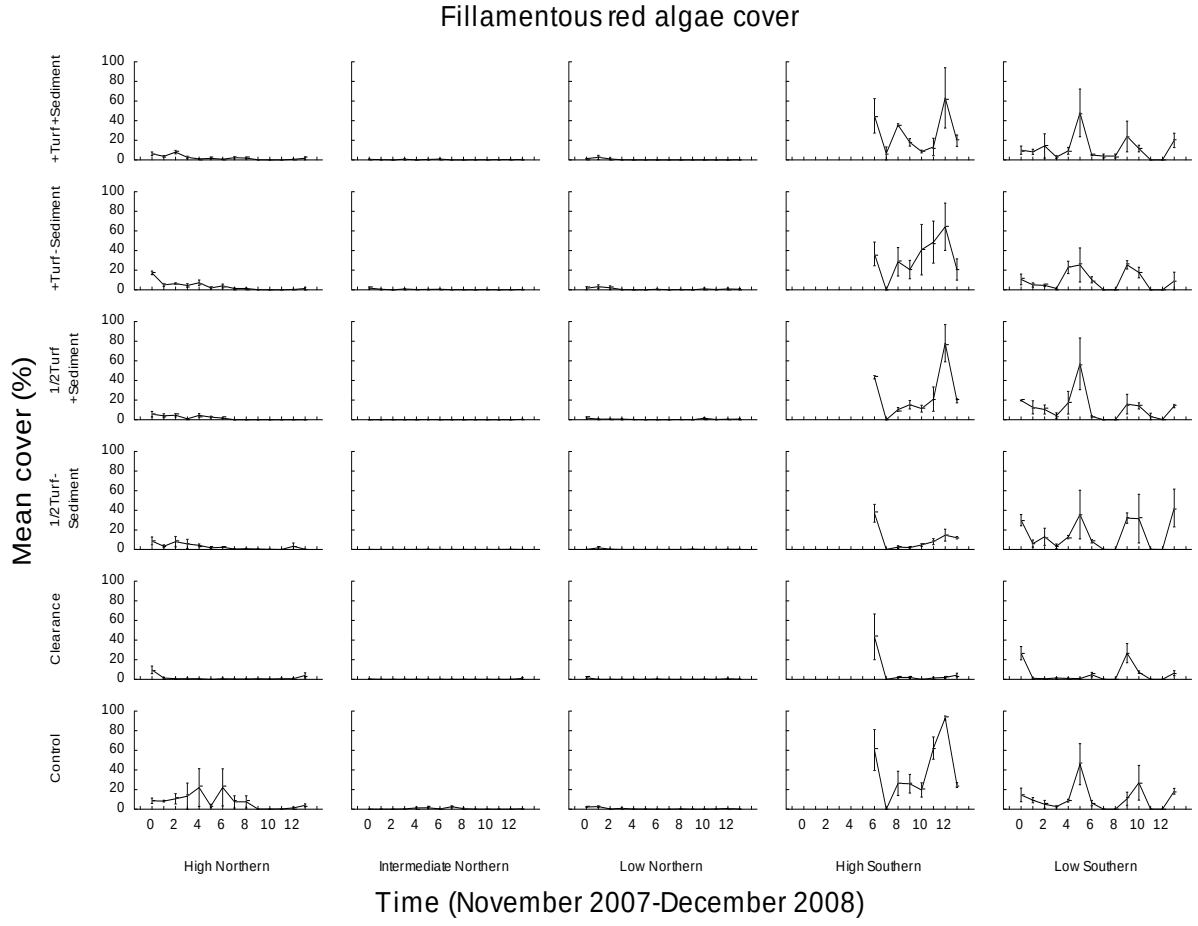


Figure 2.15 Temporal variation in the mean (±SE) percent cover of filamentous red algae between sites and treatments. Time measured in months 0=November 2007 through to 14=December 2008.

Table 2.13 Two-way ANOVA on the effect of treatment and sites on the percentage cover of encrusting and turfing red algae a) 1 month after treatment application b) 6 months after treatment application and c) 12 months after treatment application.

Effect	df	SS	MS	F	p
a) Site	4	26385.14	6596.284	10.108	**<0.001**
Treatment	5	49186.33	9837.267	15.075	**<0.001**
S*T	20	13051.01	652.550	1.973	**0.023**
Error	60	19840.17	330.670		
b) Site	4	45808.80	11452.20	10.817	**<0.001**
Treatment	5	50580.38	10116.08	9.563	**<0.001**
S*T	20	21242.78	1062.14	3.151	**<0.001**
Error	58	19552.28	337.11		
c) Site	3	40658.07	13552.69	13.064	**<0.001**
Treatment	5	47805.03	9561.01	9.216	**<0.001**
S*T	15	15561.09	1037.41	1.816	0.060
Error	48	27423.06	571.31		

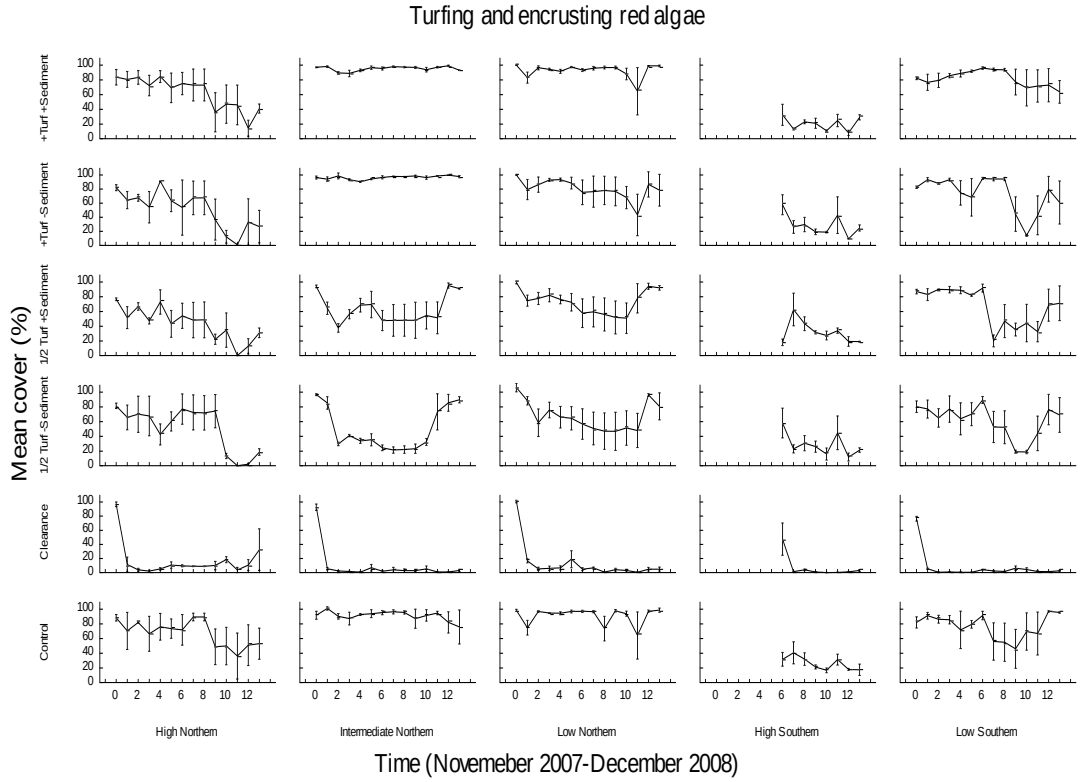


Figure 2.16 Temporal variation in the mean (±SE) percent cover of turfing and encrusting red algae between sites and treatments. Time measured in months 0=November 2007 through to 14=December 2008.

2.3.3.2. Fucoid recruitment

Despite the wide array of experimental treatments and the proximity of reproductive plants of several fucoid species, there were surprisingly little recruitment and recovery of fucoids over the 13 months of the experiment. Most recruitment occurred at the intermediate northern site for both *C. torulosa* and *H. banksii*.

Cystophora torulosa was only present on the northern side of the peninsula, accounting for the significant site and treatment interactions at 1 and 12 months after treatment application (Table 2.14 a,c) and site differences at 6 months (Table 2.14 b). Percentage cover remained low across all sites. Counts from April 2007 highlighted site and treatment differences (Fig 2.17). At the high northern site recruitment of *C. torulosa* occurred more frequently in plots where sediment had been removed or clearances made (effectively removing sediment). *C. torulosa* was not recorded at this site in pre-treatment monitoring. Recruitment at the intermediate and low northern sites was greatest under canopies in the control treatments. Other treatments although possibly having higher, initial recruitment did not show the same rate of survival (Fig 2.17) because recruits often burned off with exposure.

Recruitment of *H. banksii* was highly variable across sites and treatments, starting after 1 month due to removal during treatment application in all but control plots, and there was a gradient of initial fucoid cover in control plots (Table 2.15a). The two sites with the highest initial fucoid cover, low and intermediate northern, were the only sites that showed significant fucoid recruitment during the study (Fig 2.18), but due to such high variability within treatments there were no significant differences between treatments both within and between sites (Tukey HSD, comparisons $p>0.05$ at 6 and 12 months). The variability between treatments was most evident in the clearance and ½turf +sediment treatments at the intermediate northern site. One of the clearance treatments had 60% cover but the other two had below 10%. The same was true for the ½turf +sediment, with highest cover in one replicate at 90% and the other two below 10% after 12 months. The two plots with the highest recruitment were adjacent to each other in the experimental design.

Table 2.14 Two-way ANOVA on the effect of treatment and sites on the percentage cover of *Cystophora torulosa* a)1 month after treatment application b) 6 months after treatment application and c) 12 months after treatment application.

Effect	df	SS	MS	F	p
a) Site	4	4.566	1.142	1.107	0.381
Treatment	5	21.291	4.258	4.129	**0.010**
S*T	20	20.627	1.031	2.061	**0.016**
Error	60	30.020	0.500		
b) Site	4	2.156	0.539	2.938	**0.046**
Treatment	5	0.636	0.127	0.693	0.634
S*T	20	3.676	0.184	1.524	0.108
Error	58	6.993	0.121		
c) Site	3	5.974	1.991	2.958	0.066
Treatment	5	2.326	0.465	0.691	0.638
S*T	15	10.097	0.673	2.499	**0.008**
Error	48	12.927	0.269		

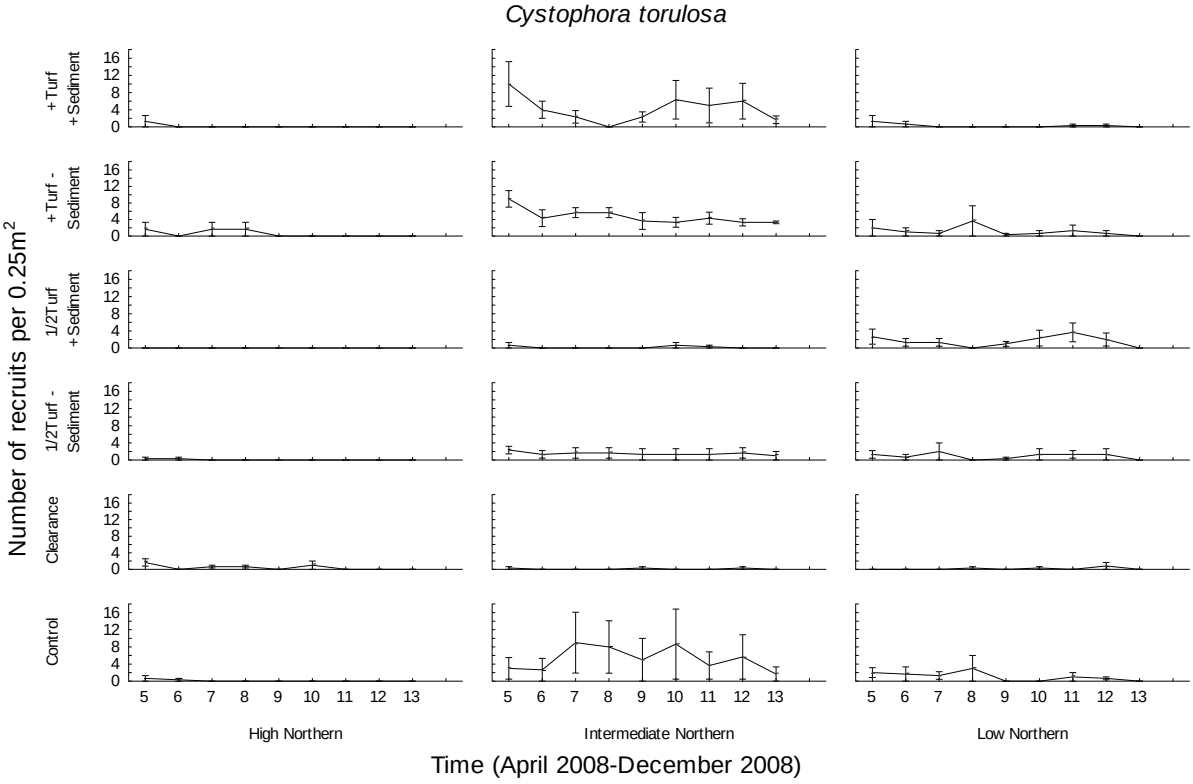


Figure 2.17 Temporal variation in the mean (±SE) number of *Cystophora torulosa* recruits per 0.25m^2 between sites on the northern side of the peninsula and treatments. Time measured in months 0=November 2007 through to 14=December 2008.

Table 2.15 Two-way ANOVA on the effect of treatment and sites on the percentage cover of *Hormosira banksii* a) 1 month after treatment application b) 6 months after treatment application and c) 12 months after treatment application.

Effect	df	SS	MS	F	p
a) Site	4	291.825	72.956	1.098	0.385
Treatment	5	1983.023	396.605	5.967	**0.001**
S*T	20	1329.430	66.472	6.012	**<0.001**
Error	60	663.427	11.057		
b) Site	4	1540.198	385.050	22.818	**<0.001**
Treatment	5	193.900	38.780	2.296	0.083
S*T	20	336.185	16.809	0.546	0.932
Error	58	1784.432	30.766		
c) Site	3	7909.94	2636.648	14.011	**<0.001**
Treatment	5	866.79	173.358	0.921	0.494
S*T	15	2822.76	188.184	0.725	0.747
Error	48	12459.50	259.573		

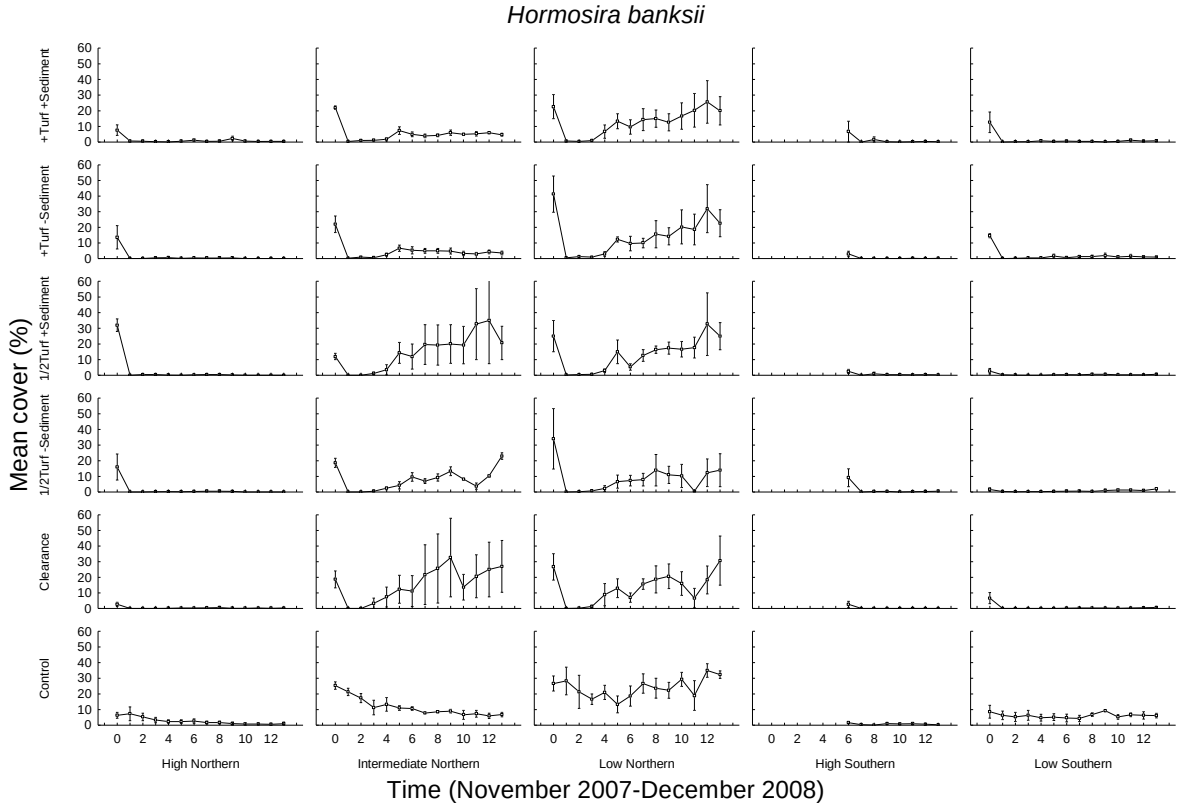


Figure 2.18 Temporal variation in the mean (±SE) percent cover of *Hormosira banksii* between sites and treatments. Time measured in months 0=November 2007 through to 14=December 2008

2.3.4 Invertebrates

Grazing gastropods did not vary significantly between treatments, although there were site differences (1 month after treatment application $F_{4,5}$=5.758, p=0.003, 6 months after treatment application $F_{4,5}$=4.535, p=0.009 and 12 months after treatment application $F_{3,5}$=26.613, p<0.001). Grazing gastropods fell into two categories: micro- and macro-

gastropods. Micrograstropods, *Eatonella* spp. and *Zeacumantus subcarinatus*, had lower abundances at the high northern site (Fig 2.19). The macrogastropods *Turbo smaragdus* and *Melagraphia aethiops*, ($F_{20,1120}$=1.601, p=0.045), were less abundant at the southern sites (Fig 2.20) with no consistent trend between treatments (Fig 2.20). Predatory invertebrates appeared only episodically during the experiment, and were dominated by the whelks *Cominella glandiformis* and *C. maculosa*. There was no consistent trend across sites or treatments and any of the time periods (Table 2.16).

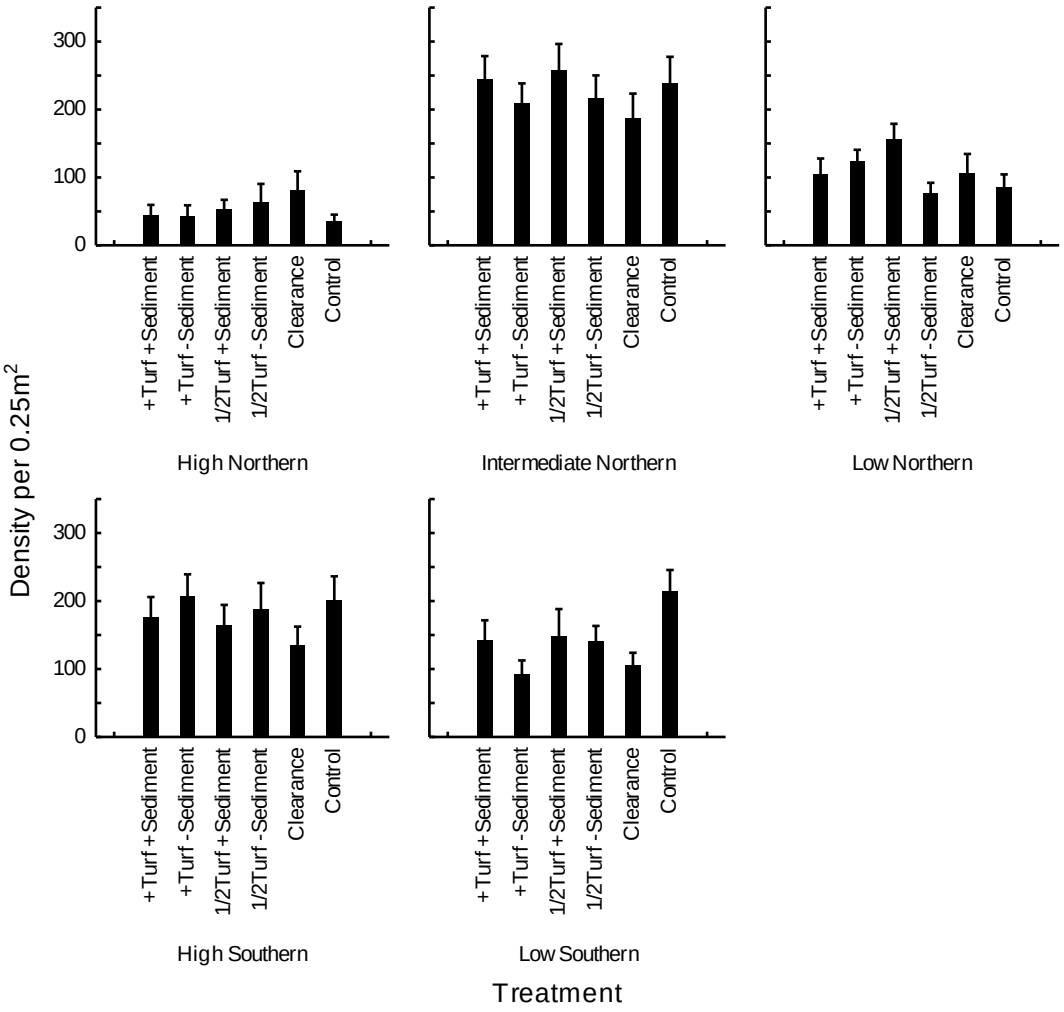


Figure 2.19 Variation in mean density of micrograstropods (*Zeacumantus subcarinatus* and *Eatonella* spp.) per metre^2 across sites and treatments. Data taken across the entire study period November 2007-December 2008.

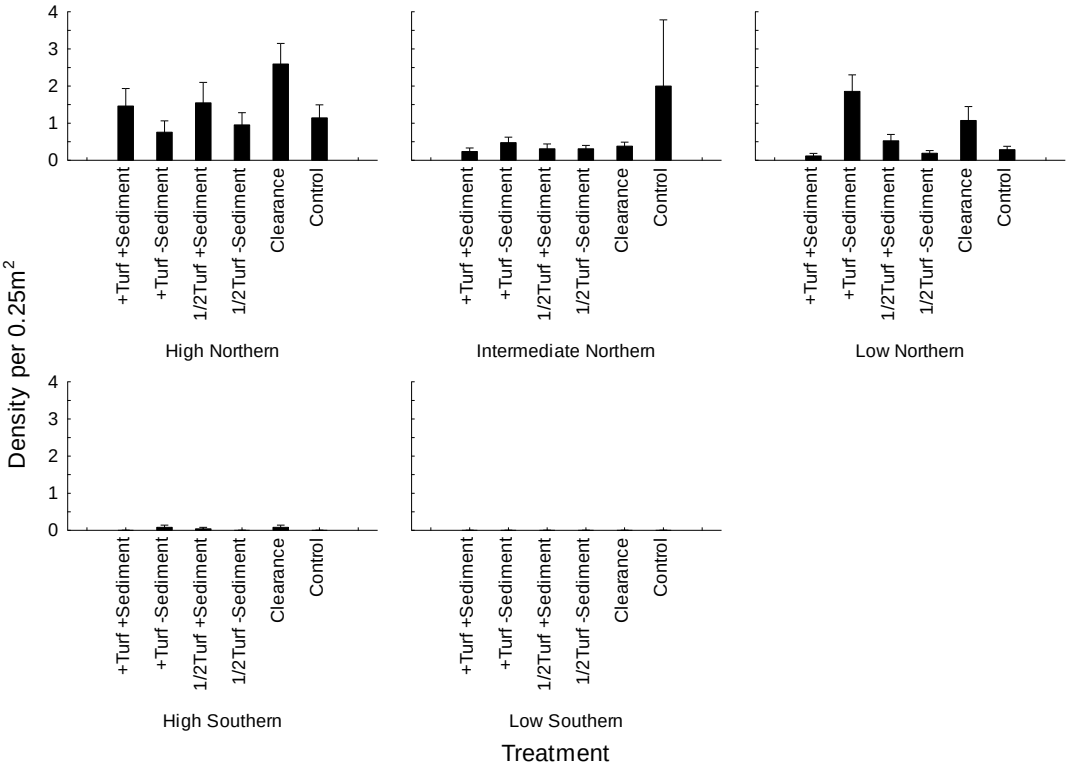


Figure 2.20 Variation in mean density of macrograstropods (*Turbo smaragdus* and *Melagraphia aethiops*) per metre^2 across sites and treatments. Data taken across the entire study period November 2007-December 2008**.**

Table 2.16 Two-way ANOVA on the effect of treatment and sites on the abundance of predatory invertebrates per 0.25m^2 a) 1 month after treatment application b) 6 months after treatment application and c) 12 months after treatment application.

Effect	df	SS	MS	F	p
a)Site	4	1.400	0.350	1.235	0.328
Treatment	5	1.389	0.278	0.980	0.454
S*T	20	5.667	0.283	1.821	0.039
Error	60	9.333	0.156		
b) Site	4	0.325	0.081	1.169	0.354
Treatment	5	0.310	0.062	0.890	0.506
S*T	20	1.390	0.070	0.864	0.630
Error	58	4.667	0.080		
c) Site	3	1.153	0.384	2.986	0.065
Treatment	5	0.792	0.158	1.230	0.343
S*T	15	1.931	0.129	1.544	0.127
Error	48	4.000	0.083		

2.3.4.1. Physical characteristics

Sediment cover and depth were significantly reduced in the -sediment plots and clearances until at least 6 months after the initiation of the experiment (Table 2.17 and Table 2.18), indicating that retreatment of plots was effective until a critical point where sediment

that had gradually accumulated became unable to be shifted by a gentle wash of water. Major differences occurred in August 2008, when there was up to 60mm of sediment covering all treatments at the high northern site (see next section) (Fig 2.21).

Bare space interacted with both site and treatments (Table 2.19). Bare space was 100% in the clearance treatments immediatly after application. The reduction in bare space as algae recruited was variable between sites, with the intermediate and low northern sites still having high percentage of bare space 13 months after clearances (Fig 2.22). At the intermediate and low northern site, bare space also increased significantly in the ½ turf treatments (Fig 2.22). In all other treatments across sites, bare space remained relatively constant over the study period except for the high northern where the smothering sediment resulted in an increase in bare space (Fig 2.22).

Table 2.17 Two-way ANOVA on the effect of treatment and sites on the percentage cover of sediment a) 1 month after treatment application b) 6 months after treatment application and c) 12 months after treatment application.

Effect	df	SS	MS	F	p
a) Site	4	19380.51	4845.128	3.975	**0.016**
Treatment	5	28755.03	5751.007	4.719	**0.005**
S*T	20	24375.36	1218.768	3.048	**<0.001**
Error	60	23992.00	399.867		
b) Site	4	5190.73	1297.68	1.586	0.216
Treatment	5	57434.69	11486.94	14.038	**<0.001**
S*T	20	16365.50	818.28	1.006	0.469
Error	58	47164.00	813.17		
c) Site	3	111.931	37.310	0.855	0.486
Treatment	5	224.403	44.881	1.028	0.436
S*T	15	654.653	43.644	0.931	0.538
Error	48	2251.333	46.902		

Table 2.18 Two-way ANOVA on the effect of treatment and sites on the mean sediment depth (mm) a) 1 month after treatment application b) 6 months after treatment application and c) 12 months after treatment application.

Effect	df	SS	MS	F	p
a) Site	4	60.020	15.005	1.732	0.182
Treatment	5	434.176	86.835	10.025	**<0.001**
S*T	20	173.243	8.662	1.310	0.208
Error	60	396.833	6.6139		
b) Site	4	79.366	19.841	1.928	0.145
Treatment	5	308.462	61.692	6.000	**0.002**
S*T	20	206.306	10.315	2.107	**0.014**
Error	58	284.019	4.897		
c) Site	3	1385.815	461.938	18.156	**<0.001**
Treatment	5	464.651	92.930	3.653	0.023
S*T	15	381.639	25.443	0.650	0.818
Error	48	1877.927	39.124		

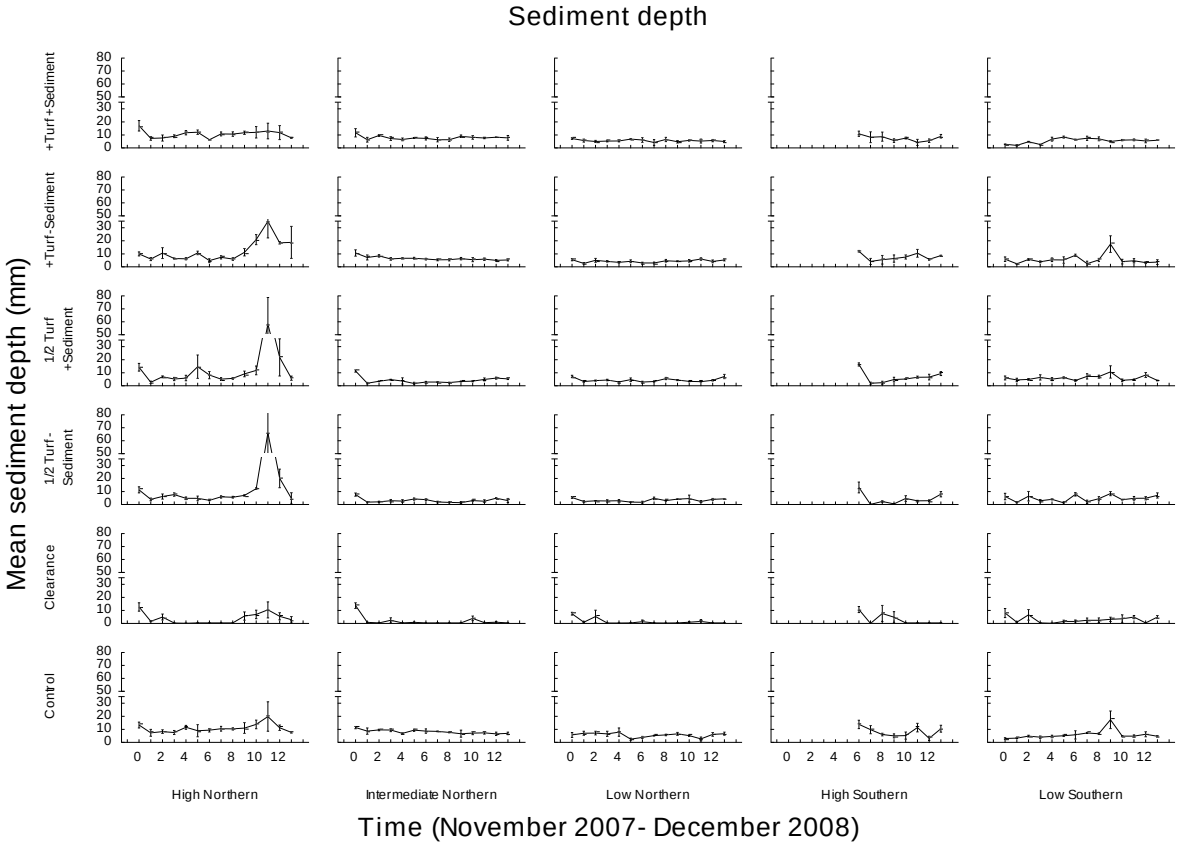


Figure 2.21 Temporal variation in the mean (±SE) sediment depth (mm) between sites and treatments. Time measured in months 0=November 2007 through to 14=December 2008.

Table 2.19 Two-way ANOVA on the effect of treatment and sites on the percentage of bare space a) 1 month after treatment application b) 6 months after treatment application and c) 12 months after treatment application.

Effect	df	SS	MS	F	p
a) Site	4	21221.58	5305.396	3.701	**0.021**
Treatment	5	26709.37	5341.873	3.727	**0.015**
S*T	20	28667.20	1433.360	3.396	**<0.001**
Error	60	25321.44	422.024		
b) Site	4	14955.90	3738.975	5.563	0.003
Treatment	5	24997.24	4999.448	7.441	**<0.001**
S*T	20	13460.11	673.005	1.395	0.162
Error	58	27980.00	482.414		
c) Site	3	60172.40	20057.47	39.337	**<0.001**
Treatment	5	2544.58	508.92	0.998	0.452
S*T	15	7648.29	509.89	1.464	0.157
Error	48	16714.01	348.21		

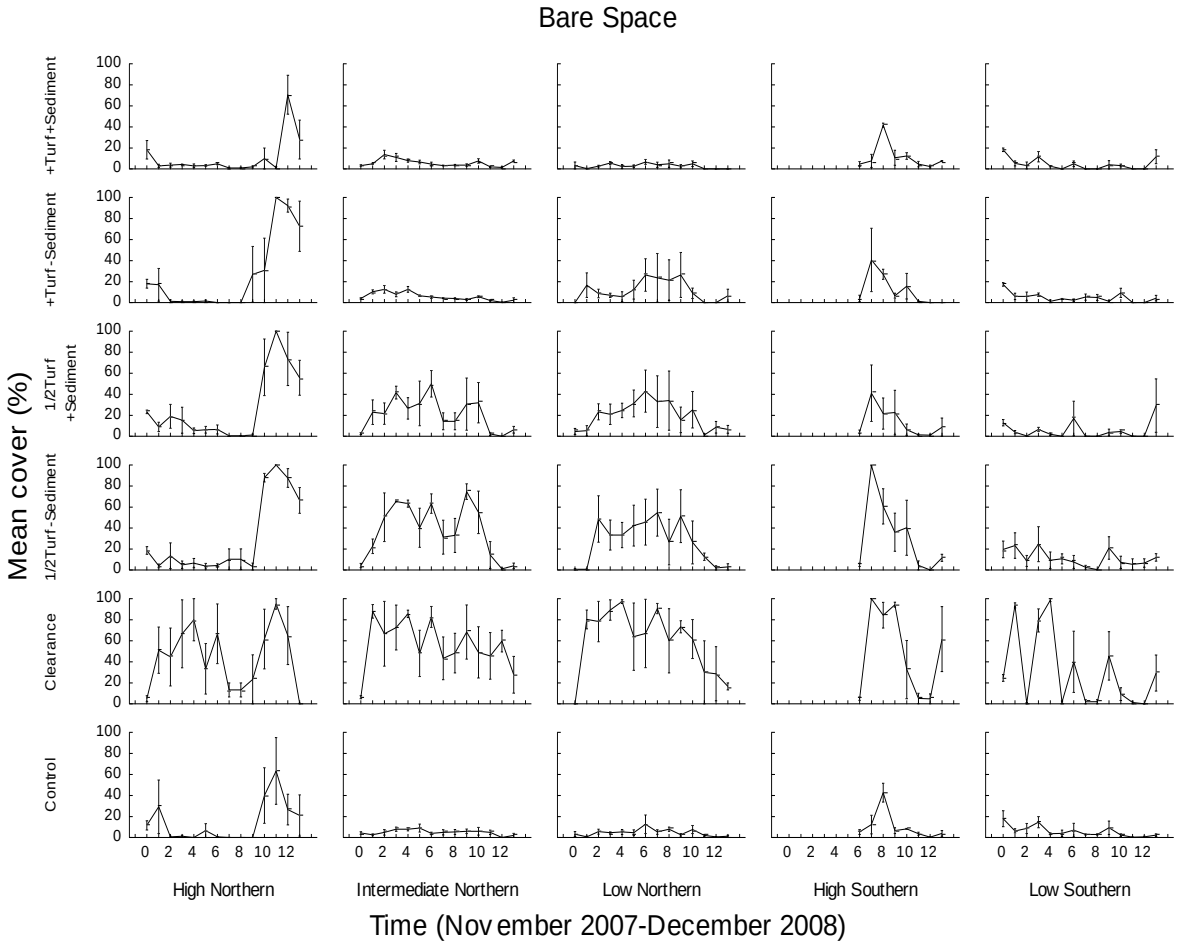


Figure 2.22 Temporal variation in the mean (±SE) percent bare space between sites and treatments. Time measured in months 0=November 2007 through to 14=December 2008.

2.3.5 Extreme weather events

The monthly rainfall was lower than average for the most of 2008, except between June and September (Fig 2.23). Two periods of intense rainfall occurred, on 30-31 July, with 142mm of rain falling, and 25-26 of August, with 125 mm of rainfall.

The impact of the extreme rainfall was dramatic at the high northern site: here the rain caused a redistribution of sediment from the landward sandy beach across the rocky platform, changing a sediment-influenced rocky shore to a soft-bottomed habitat with small rocky outcrops (Fig 2.25). Due to the large sediment flux, traps became full within 48 hours, and some were lost, so to track benthic sediment movement sediment depth measurements were taken weekly. The sediment depth was not static after the initial dump. Sediments moved on and off the site until November 2008, three months after the second storm. After this time, average sediment depth was within the range of the pre-storm period (Fig 2.24). The smothering of the substratum with sediment affected mean algal diversity for the site

(ignoring treatments). At the time of maximum burial, diversity averaged only two species (Fig 2.26), *C. officinalis* and *Ulva* spp.. *C. officinalis* cover was greatly reduced, with only tips of some of the longer branches reaching the surface. *Ulva* cover was mostly small blades that had been able to quickly colonise the new sediment cover. As the substratum returned to predominantly rocky substratum, diversity quickly returned to pre-storm levels, but was not at as high as diversity seen in November and December 2008 (Fig 2.26). The effect on species composition was variable, when comparing the algal community prior to the August storm and three months after in November (when sediment depths had returned to within there normal range). The tough Coralline turf and encrusting paint species remained unaffected (Fig 2.27). However, *H. banksii* cover was reduced; although most adults remained, all smaller recent recruits were lost (Fig 2.27). Ephemeral algae cover increased after the inundation, especially *Ulva* spp. (Fig 2.27). The only species to be lost was *Lophothamnion hirtum* (Fig 2.27).

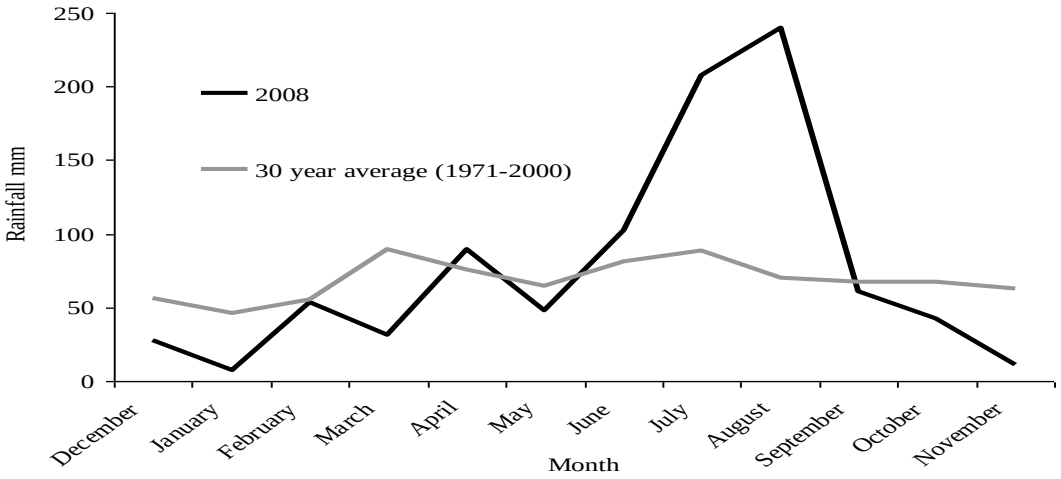


Figure 2.23 December 2007-November 2008 and 30 year average (1971-2000) rainfall (mm). Sourced from cliflow NIWA database

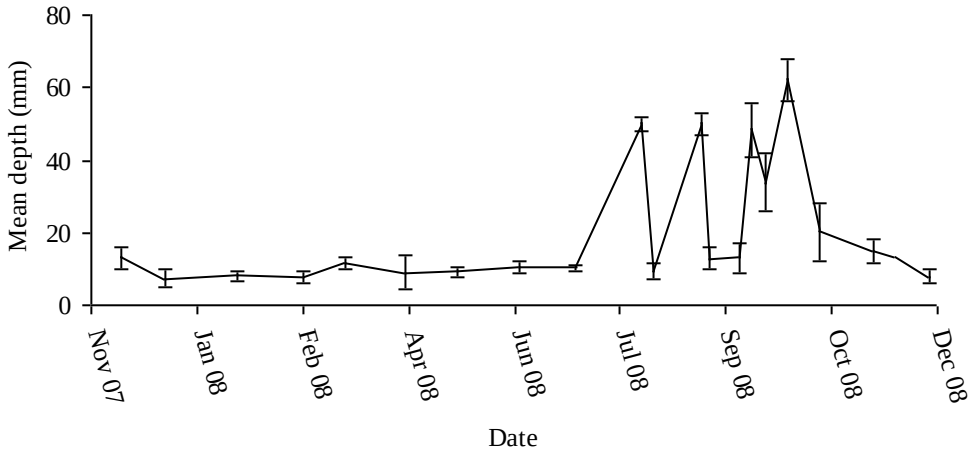


Figure 2.24 Temporal variation in mean (±SE) sediment depth (mm) at the high northern site. Data taken from control plot measurements during monitoring and extra weekly measurements during the period of increased sediment depth. Monthly measurements n=3 extra measurements during the storm n=10.

Figure 2.25 Change in the substratum type at the high northern site a) 1 July 2008 dominated by bare and algae covered rocks and b) 1 September 2008 dominated by sand, Red box indicates position of sediment trap in photograph a.

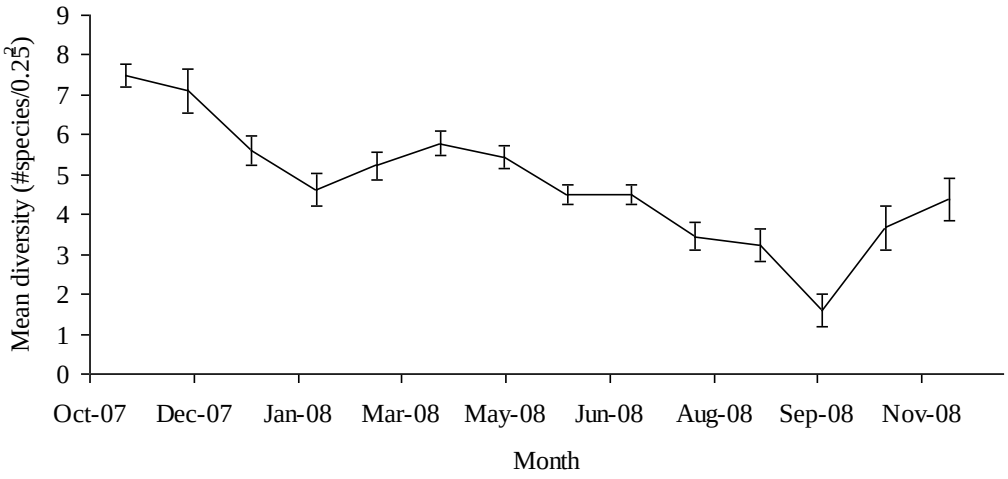


Figure 2.26 Temporal variation in mean (±SE) standing algal diversity per 0.25m^2 quadrat at high northern site. Across all treatments n=18.

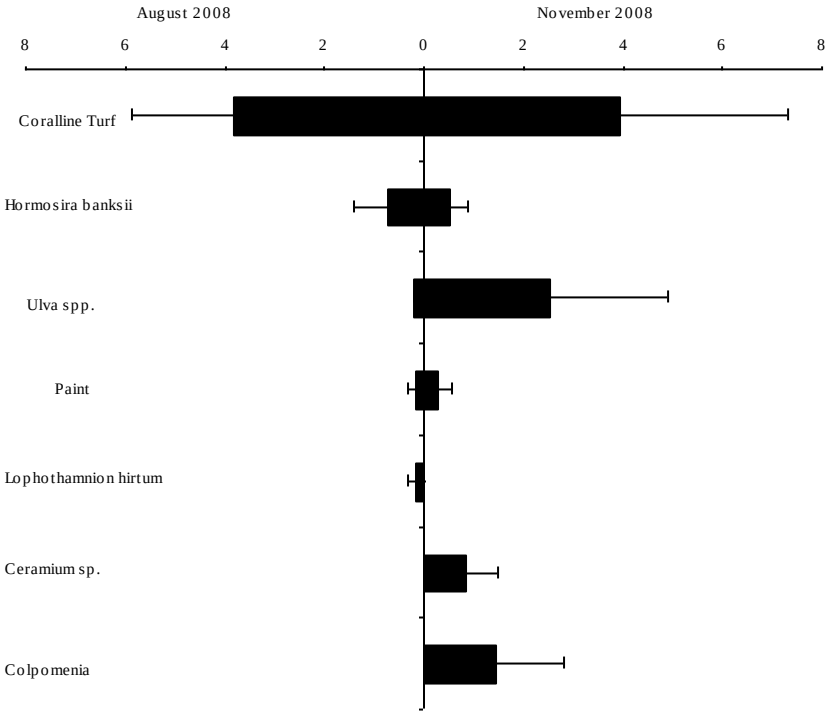


Figure 2.27 Species-rank distributions for the log-abundance of algal species in the control treatments at the high northern site in August 2008 prior to sediment burial and November 2008 once sediment depth had returned to within the long term range.

2.4. Discussion

2.4.1 Sediment environment

Sediment flux and the benthic sediment environment varied between exposures and the different sides of the peninsula, but did not fall into the gradient of sedimentation

predicted at the outset of the experiment, however, there was a gradient on either side of the peninsula. There were significant differences in flux between sites that were only ~100m apart (intermediate and low northern sites), which is consistent with the results of subtidal research done in the Mediterranean Sea, where maximal sedimentation rates varied from 28.2 g m^{-2} d^{-1} to 177.9 g m^{-2} d^{-1} between sites 100m apart (Airoldi & Virgilio 1998). Local scale variations in water flow, influenced by microtopography, small eddies and outcrops (Airoldi & Virgilio 1998), combined with small differences in exposure are likely to account for much of this variation.

On the northern side of the peninsula, flux decreased with increasing exposure, whereas on the southern side, the most sheltered site had the lowest sediment flux. The high sediment site on the northern side of the peninsula is surrounded by soft sediment shore. Therefore, although moderately sheltered, any currents and waves that pass a critical threshold for entrainment will mobilise this ready source of sediment and increase the suspended load. The close proximity of the sandy beach may also explain the higher proportion of the 100-250µm fraction at this site, and the exponential decrease away from this site (intermediate to low northern moving further from the proximal sediment source).

On the southern side of the penisula, the low sediment site is extremely sheltered. Either wave or current forces are insufficient to entrain the larger size fractions this far into the bay, or alternatively there is no proximal source of sediment. No direct current and wave strength data were taken during this study, but the southern side of the peninsula is more protected from wave action. Evidence of lower availability of larger grain sizes comes from geological studies looking at sediment budgets for the Kaikoura canyon (offshore from these southern sites). The three small rivers immediately to the south of the peninsula, Kowhai, Kahutara and Oaro, contribute approximately $1x10^6$ tonnes/annum (Griffiths & Glasby 1985) with the majority of the larger grain sizes being deposited into the canyon and the fine silts being swept towards the peninsula (Lewis & Barnes 1999).

My study has shown that there is a positive relationship between sediment flux and rainfall. Similar correlations have been reported on the Mediterranean coast where sediment cover increased with rainy weather that eroded coastlines and carried terrestrial material into the shallow subtidal zone (Airoldi & Cinelli 1997). Sediment flux around the Kaikoura peninsula seems to peak during late winter/early spring, probably due to high rainfall, snow melt and increased river flow. The influence of wind on sediment flux needs to be combined with information on currents and wave action (that suspend sediments into the water column)

where surface winds can act to move surface waters and the particles in suspension on- or off-shore (Chien & Wan 1999).

Sediment traps give a relative indication of the sediment environment among sites, but there are several caveats to their use. Traps may disproportionally lose some size fractions, and also measure re-suspension of settled particles (Airoldi 1996). Subtidal sediment traps anchored to the bottom have higher rates than those suspended in the water column, suggesting the important role of sediment re-suspension in the benthic boundary layer (Airoldi 1996). Re-suspended sediments are likely to have a greater effect on the benthic biota than suspended sediments (Airoldi 2003). The relative consistency in sediment composition between core samples and sediment traps suggests traps are relatively good at highlighting differences between sites.

The benthic sediment environment was more stable than the flux of sediments. At southern sites, *C. officinalis* and the filamentous *Polysiphonia decipiens* acted to trap sediment. Seasonal fluctuations in the abundance of *P. decipiens* coincided with fluctuations in the benthic sediment environment. The ability of turfing communities to maintain relatively consistent sediment loads, even with moderate fluctuations in sediment flux, has been shown subtidally on the Mediterranean coast, with the filamentous alga *Polysiphonia setacea* trapping the majority of sediment (Airoldi & Virgilio 1998). The branches of turfing algae form a network of ramifications protecting the sediment from removal by waves and current flows (Neumann et al. 1970). Newly arriving sediment, which is not bound into algal turfs, is more likely to be lost due to resuspension (Melville & Connell 2001). This is seen in the fluctuation in sediment depth after storms where turf had been completely buried.

The volume of sediment held within turf varies with the turf morphology, which is extremely plastic (Hay 1981, Adams 1991, Airoldi 1998, Airoldi & Virgilio 1998). Turf height was consistent over the study period suggesting that it is well adapted to the local sediment and exposure environment. Casual observations during this study found a range of turfing morphologies, but differences were between rather than within sites. For example, at the low southern site (with the lowest turf height) turf had lateral branches along the main stems whereas at the high northern site turf branches had a stalk before branching began. Whatever the branching morphology, *C. officinalis* at all sites had entangling of surface branches, and the dry weight of sediment was positively associated with that of the coralline alga. This is in contrast to studies in the Mediterranean Sea, where no relationship was found for the filamentous turfing alage *P. setacea* (Airoldi & Virgilio 1998).

2.4.2 Long term successional experiment

Subtidal experiments studying the effects of storms on temperate reefs have found that there is a two stage effect of sediments and physical disturbance; stage one are direct effects that cause a shift in community structure to disturbance-tolerant species. Stage two is the alteration of species-species interactions as a consequence of this community shift (Renaud et al. 1996). My experiments have shown both stages of community response as a result of the sediment environment and physical manipulation of coralline turfs.

2.4.2.1. Direct effects of sedimentation

The three major direct effects of sedimentation published in Airoldi's 2003 review are: 1) burial/smothering; 2) scour and/or abrasion; 3) changes to the physical characteristics of the substratum. These mechanisms are not mutually exclusive and all can be occurring at a site, affecting individual species differently.

The ranges of responses directly attributable to sedimentation are best highlighted at the high northern site. The recruitment of *C. torulosa* into the sediment clearance treatments, when the species does not occur naturally at this site, suggests that smothering of the substratum is preventing the establishment of a *C. torulosa* sub-canopy at this site. Macroalgae are affected by sediment at all life history phases, but the most critical appear to be attachment and during their juvenile phase where they are subject to burial and abrasion (Airoldi 2003). Extreme burial, like that seen during the August storm, will prevent photosynthesis and exchange of nutrients for most algae (Yanez et al. 2008). To cope with this, species must either be able to withstand burial (e.g. *C. officinalis*) or be large enough to have a portion of the biomass above the sediment (e.g. adult *H. banksii* plants).

The green ephemeral algae *Ulva* spp. were the most conspicuous differences between sites in the clearance treatments. At sites where blooms did occur there was a high covering of sediment; even at the low southern site where flux was low the silts that were present formed a blanket smothering the substratum. The sediment environment (particularly the fine grained silts) may play a role in facilitating the growth of *Ulva* spp. by either sequestering spores as a seed bank (Santelices et al. 1995)for the rapid recruitment of the algae into bare space before other species arrive or more likely, the sediments in the silts provided nutrients (Russell & Connell 2007) that *Ulva* spp. utilise more efficiently than other ephemeral species (Brush & Nixon 2003).

The sediment environment can favour certain morphological traits, one that occurs most commonly worldwide is those of filamentous forms (Airoldi et al. 1996, Russell 2005) which was seen on the southern side of the peninsula in my experiments. The genus *Polysiphonia* comprises some of the most common filamentous algae in both subtidal and intertidal zones (Rindi & Cinelli 2000). Filamentous forms have a high surface-area-to-volume-ratio that allows a greater area for photosynthesis (Balata et al. 2007b). The dominance of this morphology on the southern side of the peninsula may be result of the effects of suspended silts in the water column decreasing available light levels reaching other benthic alage (Airoldi 2003).

2.4.2.2. Alteration of species interactions

Large scale removals of *H. banksii* canopy resulted in declines of perennial and small delicately branched algae and molluscan macrograzers through the loss of non-trophic positive interactions (Lilley & Schiel 2006). The influence of the *H. banksii* canopy was evident in this study with *C. torulosa* recruits having decreased survival at the intermediate and low northern sites where canopy removal had occurred. On the southern side of the peninsula the long-term dominance of silts has led to a community with low abundance of canopy algae, resulting in lower diversity on the southern side of the peninsula. High filamentous algae cover and low fucoid abundance support the idea that the replacement of canopy forming algae with filamentous algae poses a threat to rocky shore biodiversity (Airoldi 1998, Airoldi & Virgilio 1998, Airoldi 2000, 2003, Gorgula & Connell 2004).

Long term (6 year) experiments across 6 sites in along the Californian coast tracking community recovery after total clearance treatments found that a strong ephemeral algae response early in succession at two sites delayed the recruitment of the habitat-dominating algae *Endocladia muricata* and *Mastocarpus papillatus*, (Foster et al. 2003). The clearance treatments in my study that showed a strong *Ulva* response had low recruitment of other algae and slowed recovery of *C. officinalis* and *P. decipiens*. The recovery of *P. decipiens* in the clearance treatments on the southern side of the peninsula was low compared to subtidal clearances of *P. setacea*, which regained spatial dominance quickly after experimental clearances (Airoldi 1998).

The experimental manipulation of turfing algae not only allowed the manipulation of the sediment environment, but also tested hypothesis relating to the role of *C. officinalis* and other turfing algae in the recruitment of perennial brown algae, which has been debated in the literature. Both facilitation and inhibition been experimentally shown, in different studies on a

wide variety of macroalgal species. Embryos of the fucoid *Pelvetia fastigiata* settled better in red turfs than on exposed rock (Brawley & Johnson 1991). However, epithallium shedding of encrusting corallines inhibited the recruitment of the intertidal kelps *Lessonia nigrescens* (Camus 1994). The results of my study suggest that the recruitment of *H. banksii* preferentially recruits into bare space, evidenced by the recruitment patterns seen at the intermediate northern site. Here there was significantly higher recruitment of *H. banksii* into two adjacent plots (clearance and ½turf –sediment). There was a +turf +sediment treatment within the same location that also showed *H. banksii* recruitment within the range of other treatments. A possible explanation for this is that a large recruitment pulse occurred around this area. Gamete release in *H. banksii* is sporadic and shows considerable temporal and spatial variations (Dunmore 2006). At times, large synchronistic gamete releases to occur that results in recruitment pulses. The increase in bare space in the two treatments provided space for attachment, whereas the low availability primary substratum in the third treatment plot meant that recruitment was not elevated above background levels due to a saturation effect. Indicating the a covering of *C. officinalis* may inhibit or at least slow the recruitment of fucoid algae.

The filamentous morphology of *Polysiphonia* spp. may have more of an inhibitory effect than *C. officinalis* on successful recruitment of other algal species. Although both these species trap sediments, there are fundamental differences in how this affects the primary substratum. *Polysiphonia* can reach heights of up to 10 cm and trap fine silts directly from the water column to form cohesive masses. The high surface area covered by the algae/sediment matrix smothers the substratum and prevents attachment of zygotes. *C. officinalis* is only 1-2cm tall and associated sediments seem less cohesive. Therefore, small patches primary substratum becomes available more often as sediments are moved under turbulent flow (Chien & Wan 1999). Inhibition of zygote recruitment has been shown in subtidal *P. setacea* (Airoldi 1998) and the most likely mechanism is the sediment trapping ability of this species (Kendrick 1991).

2.4.2.3. Response of turfing algae to disturbance

Since the crucial role of turfing coralline in sediment retention has been found in several studies (Kendrick 1991, Kelaher et al. 2001, Huff & Jarett 2007) with consequential effects on community assemblages, understanding the rate and mechanisms of recovery after partial or complete removal of biomass is important for understanding the stability of the

benthic sediment environment. The total clearance treatments at the high northern site where recovery was greatest, have a complex topography with deep crevices and is likely that scraping did not remove all of the basal plates, the primary mechanism for geniculate coralline recovery (Chapman & Underwood 1998). Coralline algae also showed reductions in cover in the ½turf treatments. As stated above, turfing algae show considerable morphological plasticity. They also have the ability to redirect photosynthetic pigments vertically and horizontally (Hay 1981). Photosynthetic pigments are concentrated in the apex of turf branches as there is significantly lower light penetration to the lower branches (Hay 1981). Therefore, reducing turf height would have reduced the efficiency of *C. officinalis* photosynthesis. The reduction in cover may be a response to this, with the algae redistributing cellular energy to less damaged areas to build up photosynthetic pigment. This could have caused the die back in other areas until repair mechanisms have worked and lateral vegetative propagation can allow expansion of percentage cover (Stewart 1983). The reduction in cover in the turf treatments showed a quicker recovery than the clearance treatments, since *C. officinalis* maintains its spatial dominance by encroachment of lateral branches (Airoldi 1998). The numerous small patches of *C. officinalis* remaining after turf height was reduced likely aided in the more rapid recovery than seen in total clearances.

2.4.3 Extreme weather events

Increased sedimentation after storm events and spatial variation in the magnitude of this increase has been reported previously in long term sediment measurements along the Mediterranean coast (Airoldi 1998), the effects of these storms were also highly localised. Sediment burial did not alter species composition, just the relative abundances of those species. The movement of sediment on and off the site as natural levels returned would have been important to survival of algal thalli, by allowing short periods where photosynthesis and nutrient exchange could occur (Trowbridge 1996), however the movement of these sediments induces scour of algal thalli, causing a partial loss of biomass for most species (i.e. a reduction in percentage cover) (Vaselli et al. 2008). The only species lost was *Lophothamnion hirtum* and this is more likely due to natural seasonal fluctuations (Mei & Schiel 2003). *C. officinalis* cover did not alter significantly, showing its resilience to short term smothering and sedimentation in general due to its tough thalli (Daly & Mathieson 1977). The reduction in *H. banksii* cover showed the sensitivity (especially of settlers and recent recruits) of this canopy forming species to dramatic change, in the sediment environment (Schiel et al. 2006). The

loss of recruits means that as the canopy dies off there may be a lack of juvenile recruits to replace them. Recovery from the loss of *H.* banksii is slow and this has important impacts for the structure of the rest of the community (Lilley & Schiel 2006). Ephemeral algae quickly colonised after sediment removal (*Ulva* spp. and *Colpomenia* spp.) showing the same response as the clearance treatments in the successional experiments. The other species that appeared after the sediment was removed was *Ceramium* sp.. This species has a filamentous form similar to *Polysiphonia* species and is adapted to high sediment environments and is ephemeral in response to disturbance (Adams 1994).

2.4.4 Summary

The sediment environment showed significant variation both spatially and temporally and this had a direct influence on the community structure. The differences between the sediment flux and benthic environment highlight the need to quantify both when reporting the effect of the sediment environment on community structure. If sedimentation increases, as predicted the results of this study suggest there will be a shift in community composition to an algal community dominated by filamentous and turfing forms punctuated by blooms of ephemeral algae. The storm events of 2008 provided an added dimension to the experimental work, showing that there was a level of resilience in the community. However, any loss of recruits during that period may have longer-term impacts on the community. If storm frequency and erosion increase as predicted; related changes in the sediment environment may become more frequent, diminishing the intervals where algal recruits can reach a critical size where they are resistant to burial.

Chapter 3. Effects of sediment and turfing algae on early life history stages of fucoid algae

3.1. Introduction

By the time a fucoid recruit has reached a size where it is visible in field experiments, it has passed through two critical phases, attachment and early post-settlement survival (Amsler et al. 1992). Therefore, in addition to manipulative field experiments (Chapter 2), lab experiments were required to clarify the effect of sediment and the turfing environment on settlement before other life history characteristics come into play. To fully understand the effects of the sediment environment on the structure of fucoid populations, I wished to decouple the effects of sediment on settlement and early post-settlement survival.

Because fucoid algae show significant fluctuations in reproductive output (Schiel et al. 2006), even an ephemeral presence of sediment during reproductive periods of the year can have a dramatic effect on recruitment success (Schiel et al. 2006). Early post-settlement stages of algae are most likely to be affected by sediment (Valdas et al. 1992, Airoldi 2003). Sediments may prevent attachment by smothering available substratum (Valdas et al. 1992), altering light penetration to newly settled zygotes (Devinny & Volse 1978, Chapman & Fletcher 2002), or causing the development of anoxic areas (D'Antonio 1996, Airoldi 2003).

Attachment is recognised as one of the most important events in the life cycle of intertidal algae (Hardy and Moss 1979). Early research on the laminarian alga *Macrocystis pyrifera*, showed that sand densities of 10 mg/cm^2 prevented spore attachment to a slide and reduced the probability of spore survival (Devinny & Volse 1978). This study also showed that smothering and abrasion of recently attached germlings occurred, with the switch between the two depending on water motion (Devinny & Volse 1978). Their effects in combination were more harmful than either alone (Devinny & Volse 1978). Schiel *et. al.* (2006) showed that even a thin layer of sediment can prevent *Hormosira banksii* and *Durvillaea antarctica* zygotes from reaching an artificial substratum.

To test the effects of different sediment and disturbance regimes on the survival of fucoid zygotes, zygotes were settled in laboratory conditions onto artificial substrata that were placed into the field and monitored for survival (c.f., Taylor & Schiel 2003, Dunmore 2006). Similar to previous experiments in turf (Thompson 2004), I used lengths of cotton culture string, which had the advantage of being able to be settled in a laboratory, then pushed into turfs and sediment in the field.

This chapter tests the hypotheses 1) that different size-fractions and abundance of sediment affect the attachment of *Hormosira banksii* and *Cystophora torulosa* zygotes under laboratory conditions and 2) that alterations to the sediment environment and disturbances to the turfing community affect early post-settlement survival of laboratory-cultured fucoid zygotes placed into the natural environment.

3.2. Methods

3.2.1 Zygote solution

Zygote solutions were prepared following the methods of Dunmore (2007). Reproductive algae were collected from the field and refrigerated for ~3 days. These were then placed into direct sunlight or under heat lamps for ~2 hours to induce gamete release. Gametes were washed from the seaweed with filtered (1µm), UV-treated seawater (treated seawater was left to settle at 16°C for at least a week prior to use). The water and seaweed were agitated for several minutes and left for a further 30 minutes to promote fertilisation. The zygote slurry was passed through a plankton mesh filter (100µm *H. banksii*, 250 µm *C. torulosa*) that allowed zygotes to pass but removed debris.

3.2.2 Laboratory-based fucoid settlement experiments

A series of laboratory based experiments was done to examine the settlement of *C. torulosa* and *H. banksii* embryos under different sediment conditions. Artificial plates were used to test the ability of fucoid zygotes to settle in different sediment environments. These provided a homogenous substratum for settlement. After 48 hours embryos are easily visible under a binocular microscope. Previous research has shown that fucoid zygotes settled, attached and survived well on fibrolite ('Hardiflex™') plates (Taylor & Schiel 2003, 2005, Dunmore 2006, Schiel et al. 2006). The square fibrolite plates were 110 x 110 mm and 7 mm thick. After 48 hours embryos are easily visible under a binocular microscope.

Fibrolite plates were placed into two-litre plastic containers and covered with 500mL of filtered and UV treated seawater. Varying amounts of sediment were added in a seawater slurry to a 78.5cm^2 area on the plate using a PVC tube (10cm diameter) to prevent sediments from dispersing until they had settled. Sediment was collected from the sediment traps used in Chapter 2 and dried for 48 hours at 65^{o}C. The treatments were: control (no sediment), 50% covering of fine silt (<25 µm) with a dry weight of 0.15g (19.1g/m^2), 100% covering of silt

with a dry weight of 1.5g (191.1g/m^2), 50% covering of fine sand (<250-100 µm) with a dry weight of 0.5g (63.7gm^2), 100% covering of fine sand with a dry weight of 3g (382.2g/m^2). Four replicates of each treatment were used for each of five trials. Once the sediment had settled, 25mL of zygote solution was poured over each plate. The plates were left for 48 hours under 12:12 full spectrum light conditions and constant temperature of 15-18^{o}C. Attached zygotes were counted under a binocular microscope; five 1cm^2 sub-samples were taken from each plate to estimate zygote density. Zygotes on the plate and on the sediment were counted. Zygotes attached to the silt were visible without removing the sediment from the plate. If the embryos fell between sand grains and became difficult to identify, subsamples were removed from the plate using pipettes. These were searched while in a single thin layer on a plastic petri dish.

3.2.3 Field-based early post-settlement experiment

This experiment was done with the two regionally dominant fucoid algae, *H. banksii* and *C. torulosa*. Zygote solutions (see 3.2.1 above) were poured over pre-soaked (24 hours) cotton culture strings that were covered with approximately 1cm of filtered seawater. The strings were 50mm in length and 2.5mm in diameter (Fig 3.1). The strings were attached to the rock surface by a 40mm stainless steel coach screw through a loop at each end. The bolts were anchored into the rock surface with 8mm nylon ramset™ Rawl plugs. This method was effective in embedding the strings into the turfing community. However, it also allowed strings to be removed for counting the developing germlings without disturbing the attached algae. Variations in gamete production meant that initial densities both within and between the two fucoid species were variable. Prior to deployment in the field, settled strings were cultured for at least one week. Cultures were maintained in a temperature-controlled facility (15-17^{o}C) under 12:12 light-dark cycles and a 30w cool white light (Sylvania Luxline plus 2400 lumen). Seawater was changed after 24 hours and every three days thereafter, ensuring that the strings were covered with at least 1cm of seawater at all times. After the first water change, 20mL of modified Provasoli's medium, (see Appendix 1 for nutrient concentrations) (West & McBride 1999) was added per litre of seawater. Prior to the Time-0 germling counts, the strings were agitated gently in seawater to remove loosely attached germlings.

Figure 3.1 Cotton culture string amongst the turfing algae. This is a 1/2 turf + sediment treatment. The string is 5cm long.

After strings had been in culture for at least a week they were randomly assigned to one of six treatments. Each treatment had three replicates, and five separate outplanting trials were run for each of the two fucoid species. Treatments were the same as for the long-term successional experiments (Chapter 2): +Turf +Sediment, +Turf –Sediment, ½Turf +Sediment, ½Turf –sediment, clearance and controls. Controls for this experiment were culture strings maintained under laboratory conditions (15^{o}C and 12:12 light cycles with a 30W cool white light (Sylvania Luxline plus 2400 lumen)). The experiment was established in the low *Hormosira* zone in an area of high sedimentation, adjacent to the high northern site in Chapter 2.

A binocular microscope was used to monitor the density of germlings on strings. These were either counts of the entire string, or 5 x 2.5mm^2 subsamples, if high densities made total counts impractical. Counts were made on Days 0, 2, 5, 8 and 14, by taking them back to the lab; they were kept moist and returned to their treatments within one low tide period.

3.2.4 Data analysis

The laboratory-based zygote settlement experiments and the field-based early post-settlement experiments were analysed using ANOVA models. Prior to ANOVA, Cochran's tests were performed and, where necessary, data were log-transformed to stabilise variances (Sokal & Rohlf 2003). All analyses were done using *Statistica* 7.1.

3.3. Results

3.3.1 Laboratory-based zygote settlement experiments

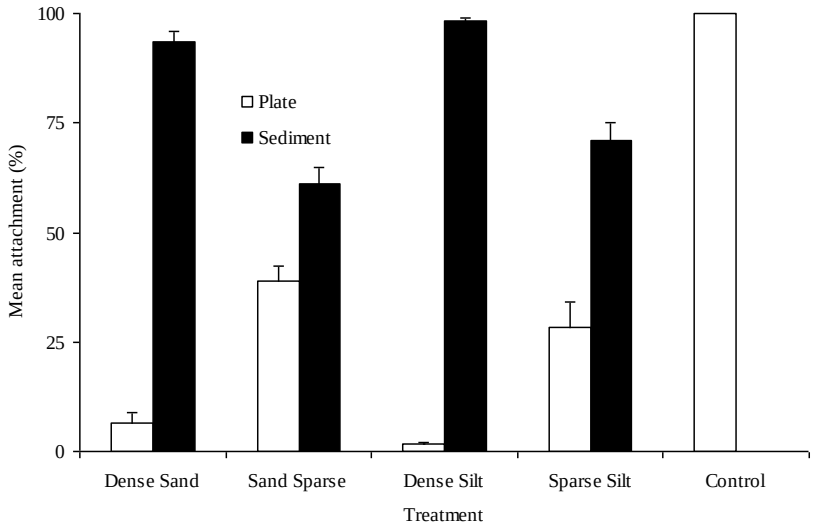
There were clearly differences between the two species in their ability to settle onto plates through various layers of sand and silt, though high variance ment differences were often non-significant (Fig 3.2). In sparse sand and silts most *H. banksii* zygotes made it through to settlement onto the plates but in all cases, *C. torulosa* attached mostly to the sediments. This resulted in a significant species x treatment interaction (Table 3.1). High coverings of either sand or silt resulted in a >90% reduction in the percentage of zygotes attaching to the artificial substratum (Fig 3.2). There was no significant difference between sediment type (*C. torulosa*: Tukey HSD, p=0.960 and *H. banksii*: Tukey HSD, p=0.964) or between species (sand: Tukey HSD, p=0.984 and silt: Tukey HSD, p=0.925). The sparse sediment treatments showed significant differences between species (sand: Tukey HSD, p=<0.001 and silt: Tukey HSD, p=<0.001), with *C. torulosa* having on average 24% more zygotes attached to the sand and 29% more attached to silt than *H. banksii* (Fig 3.2). Within species there was no difference between sediment types with a sparse covering (*C. torulosa*: Tukey HSD p=0.386 and *H. banksii*: Tukey HSD p=0.938).

The combined density of zygotes attached to the sediment and to plates was not significantly different from the control treatment settlement density for *C. torulosa* ($F_{4,95}$ = 1.212, p=0.311) and *H. banksii* ($F_{4,95}$ = 0.577, p=0.680).

Table 3.1 Two-way ANOVA of the percentage of embryos attached to sediment grains. Control plates (no sediment) were excluded. 48 hours post-settlement

Effect	Df	SS	MS	F	p
Species	1	3.533	3.533	39.04	**<0.001**
Treatment	3	19.520	6.507	71.90	**<0.001**
Spp*Treatment	3	3.444	1.148	12.69	**<0.001**
Error	152	13.755	0.090		

a) *Cystophora torulosa*



b) *Hormosira banksii*

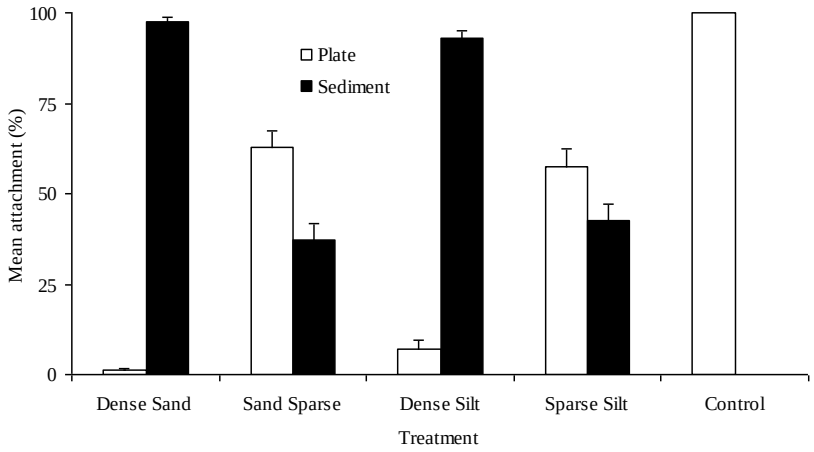


Figure 3.2 Mean percentage (+SE) of a) *C. torulosa* and b) *H. banksii* embryos attached either to plates (white bars) or sediment (black bars), 48 hours post-settlement.

3.3.2 Field-based early post-settlement experiments

The two fucoid species showed significant differences in the rate of survival and interactions with treatments throughout this experiment. *H. banksii* survived better across all treatments than *C. torulosa* (Fig 3.3 a, b). The responses of these species to the treatments were also different. The survival of *C. torulosa* initially decreased as disturbance of both turf and sediment loads increased, with poorest survival in total clearances with 9% mean survival after 2 days. This species initially did best in the +turf +sediment with 46% mean survival after 2 days, most likely because of moisture retention. However, by Day 8 no *C. torulosa* germlings were surviving in any of the field treatments (Fig 3.3a). *H. banksii*, showed no

significant differences among the field treatments over the entire experiment (Fig 3.3b) Zygotes of this species are much smaller than those of *C. torulosa* and they could be seen microscopically attached deep within the matrix of culture strings, whereas *C. torulosa* attached to the surface. There was a significant interaction between species after 5 days (Table 3.2), with significantly higher survival across all treatments for *H. banksii* (37% in the ½turf +Sediment to 48% in +turf +sediment) than *C. torulosa* (0.8% in clearance treatments to 22.5% in the +turf +sediment treatment). After 5 days for *C. torulosa*, survival in the clearance treatment was significantly lower than in the +turf +sediment and +turf –sediment treatments (Tukey HSD, p=<0.050). After 14 days, survival of *H. banksii* embryos was still greater than 21% (Fig 3.3b) with no significant difference among treatments (Table 3.3).

The timing of deployment of string outplants (trials) significantly affected the response of treatments after 5 days for *C. torulosa* (Table 3.4). There was no significant effect of trials for *H. banksii* after 14 days (Table 3.5).

Table 3.2 Two-way ANOVA of species and treatment differences in the survival of zygotes. Time fixed at 5 days (lab control excluded).

Effect	Df	SS	MS	F	p
5 days					
Species	1	28903.07	28903.07	96.159	**<0.001**
Treatment	4	2219.24	804.81	2.677	0.035
Spp*Treatment	4	12590.29	312.57	1.0040	0.390
Error	110	33063.49	300.58		

Table 3.3 ANOVA of treatment differences in the survival of *Hormosira banksii* zygotes. 14days (lab control excluded).

Effect	Df	SS	MS	F	p
Treatment	4	946.58	236.64	0.495	0.740
Error	55	26308.01	478.33		

Table 3.4 ANOVA on the trial and the effects of the effects of treatments on the survival of *C. torulosa* after five days (lab controls excluded).

Effect	Df	SS	MS	F	p
Trial	4	3691.477	922.869	5.096	0.002
Treatment	3	3399.304	1133.101	6.257	0.001
Error	52	9416.540	181.087		

Table 3.5 ANOVA on the trial and the effects of the effects of treatments on the survival of *H. banksii* after 14days (lab controls excluded).

Effect	Df	SS	MS	F	p
Trial	4	946.58	236.644	0.481	0.750
Treatment	3	726.34	242.114	0.492	0.689
Error	52	25581.67	491.955		

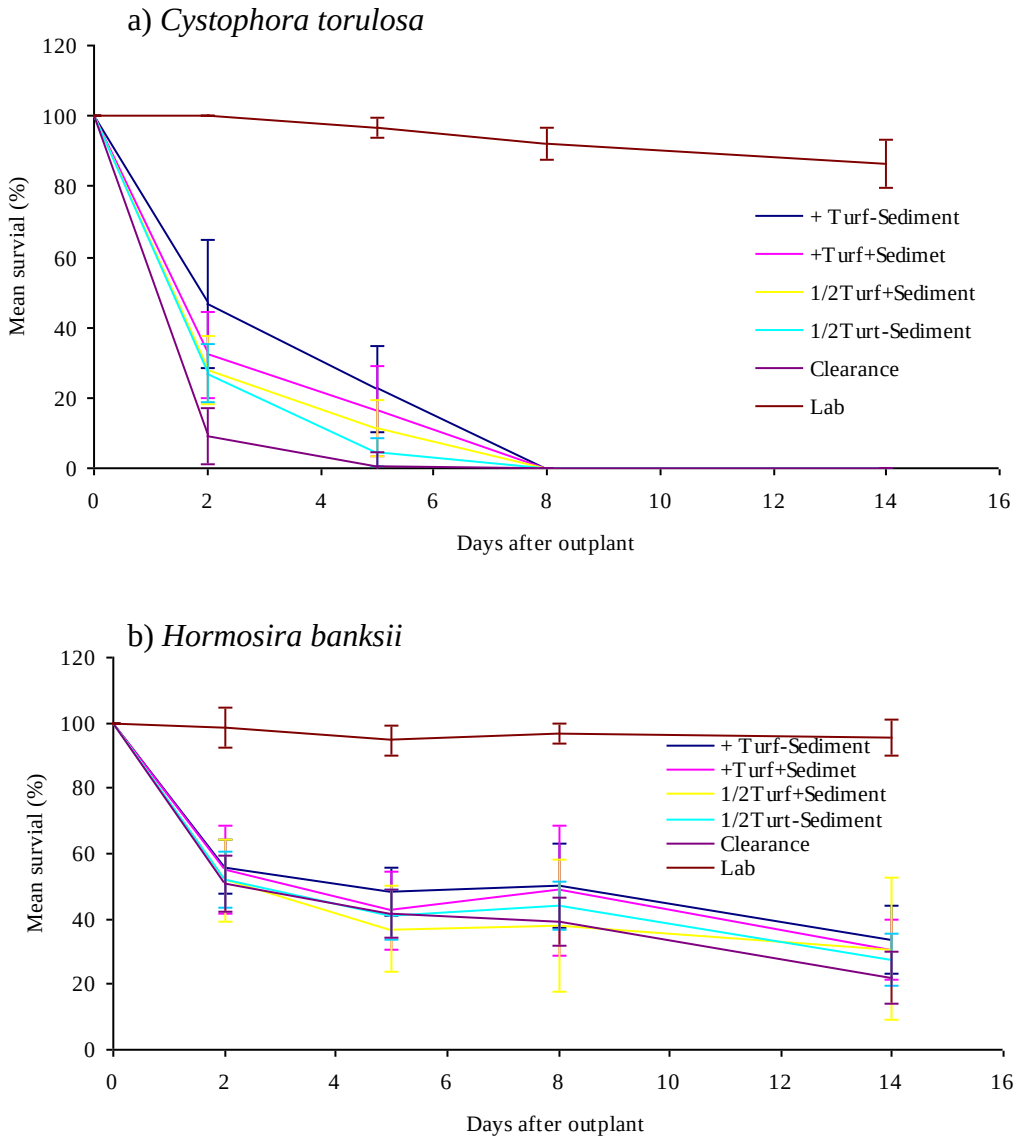


Figure 3.3 Mean survival (±SE) of zygotes of a) *C. torulosa* and b) *H. banksii* on culture string in field-based early post-settlement experiments.

3.4. Discussion

The sediment environment influenced both the attachment of fucoid zygotes and early post-settlement survival. These experiments highlighted key differences between species in their method of attachment and subsequent interactions with the abiotic environment.

3.4.1 Attachment

My experiments highlighted the differences between species in attaching to the substratum in the presence of sand and silt. These differences are due to the physical characteristics of the zygotes and the time they take to adhere (Schiel et al. 2006). Zygotes produce a mucilage that attaches them to the substratum initially. However, the "stickiness" and rate of hardening of this mucilage is species-specific (Taylor & Schiel 2003). Other experiments have found that *C. torulosa* attaches more quickly and firmly than *H. banksii* (Taylor & Schiel 2003). These differences may explain why a greater percentage of *H. banksii* zygotes attached to the substratum: their lower stickiness meant that they rolled between large grains, and adhered to the substratum below. *C. torulosa,* however, was more likely to attach to the first object it came in contact with, which was usually sand and sediment.

Decreased attachment to primary substrata in the presence of sediment has been shown in other fucoid algae. Schiel *et al* (2006) found that *Durvillaea antarctica* zygotes had significantly less attachment to plates than *H. banksii* when a thin layer of sediment was present. Irving *et al.* (2009) covered petri dishes with sediment (from below fucoid stands), added *Cystoseira barbata* zygotes and recorded those attached after two weeks. He used a greater amount of sediment than in my study (1398g/m^2 *(pers comm.)*), which was consistent with sedimentation rates in the natural environment. Settlement densities on sediment-covered dishes were only 1-5% of control dishes (Irving et al. 2009).

Different grain sizes of sediment have different physical and chemical properties (Chien & Wan 1999) and, therefore, were expected to have different effects on the attachment of fucoid embryos. Zygotes that settled onto silts became completely smothered and no elongation was evident after 48 hours, whereas zygotes attached to sand grains showed good development similar to those attached to the substratum. It seems clear that the loss of embryos is not because of the sand abrasion, but from attaching to grains that are washed away (Devinny & Volse 1978). Therefore, if zygotes settle on sand grains bound within a turfing matrix it is possible they will survive if the rhizoid attaches to the substratum before the sand is washed away.

A sparse covering of sediment, regardless of whether it was sand or silt, had inverse effects on the attachment of the two algal species. Sparse sediment cover resulted in less *C. torulosa* attaching to plates, but less *H. banksii* attaching to the sediment. Sand remains as individual grains, so it was predicted that zygotes would fall into the relatively large interstitial spaces between the grains (Chapman & Fletcher 2002) and have more chance of reaching the substratum. Silt particles, however, form chemical bonds between individual grains to form flocs (Chien & Wan 1999). These smother the substratum more effectively than sand, even at lower densities. The properties of sediment in different size fractions can have other effects on early post-settlement stages. For example, fine sediment in various quantities has been shown to decrease survival of *Fucus serratus*. Chapman and Fletcher (2002) showed of that a 1mm layer of fine (<63 µm) sediments allowed greater survival and growth of settled *F. serratus* than either a thicker (3mm) layer of fine sediment, or mixed layers of coarse (250-350 µm) sediment. These differences were attributed to increased sediment cover (particularly as grain size decreased) reducing diffusion of essential nutrients and waste products. Therefore, although sediment type showed no significant difference in attachment rates, it may influence early post-settlement survival.

3.4.2 Post-settlement survival in the field

The differences in the manner in which zygotes of *H. banksii* and *C. torulosa* attached to the string substrates translated into differences in post-settlement survival. *C. torulosa* embryos were attached to the string surface; therefore, differences in survival were a result of micro-scale variations in abiotic environments between treatments. As microscopic embryos, the sediment-clogged turf environment will provide protection from desiccation during aerial exposure (Hay 1981, Airoldi 2003). Reduction in height and removal of sediment from the turf would likely reduce its moisture retention capability. Beneficial effects of corallines have been shown in the survival of other canopy algae. Benedetti-Cecchi and Cinelli (1992) found greater settlement of *Cystoseira brachycarpa* in fleshy turfing algae than in corallines, but recruitment was greater in the corallines. Attachment was not measured in this study, but early post-settlement survival falls into the recruitment phase of survival. Because embryos bound in sediments in algal turfs are relatively stable, sediment abrasion is unlikely to cause dislodgment (Chapter 2, Airoldi 1998). However, strings placed into the clearance treatments were likely to have abrasive sand moving over them, increasing the rate of mortality (Devinny & Volse 1978, D'Antonio 1986). It was hypothesised that both species would survive as

embryos within the turfs because its moisture retention would minimise the effects of desiccation on early post-settlement survival (Valdas et al. 1992). However, after 8 days, no *C. torulosa* embryos survived on the strings, so any of the beneficial effects of algae turfs only acted to slow the rate of loss. The micro-scale differences in abiotic conditions vary with exposure to waves, wind and solar radiation during the experiment. This may explain the significant interaction between timing of the outplant and treatment on *C. torulosa* survival.

H. banksii survival was not affected by micro-scale variation in conditions between treatments because the embryos attached deep within the weave of the string. Higher survival rates of *H. banksii* embryos in the mid-low intertidal, compared to other fucoid algae and shore heights, have been reported previously, (Dunmore 2006). Her experiments showed in the low shore zone that desiccation stress, although important for *H. banksii* survival, had less of an influence than grazing. Therefore, the lack of significant differences between treatments could also be partially explained by a grazing effect. Because grazing was not controlled for in this experiment it is expected to be consistent across treatments. No effect of grazers was found in these treatments from Chapter 2 and the micrograzers *Zeacumantus* spp. were seen on or around the strings during the experiment, but no differences between treatments were obvious. The different degrees of attachment to the string seen in this experiment may also occur naturally in terms of attachment to turfing algae; *H. banksii* may bury further into the sediment and turfing environment, thus protecting it from desiccation (Airoldi 2003), abrasion (Devinny & Volse 1978) and size-selective grazing (Dunmore 2006).

3.4.3 Summary

Sediment cover on primary substrata can have dramatic effects on the attachment of fucoid zygotes. This can have long term effects on community structure because sediments are often a constant part of benthic surfaces. Furthermore, sediments can be seasonally abundant during fucoid settlement seasons (see Chapter 2). If zygotes manage to attach to the substratum under high sediment conditions, the embryos then pass through another set of survival barriers during early post-settlement interactions. The ephemeral nature of the arrival and departure of sediments may contribute substantially to the patchiness of algal recruitment and adult populations on rocky shores (Schiel et al. 2006).

Chapter 4. Role of nutrients and sediments and grazers

4.1. Introduction

Concurrent impacts on coastal systems mean additive and synergistic effects must be considered when exploring the effects of anthropogenic stressors on rocky shores (Thompson et al. 2002). Increases in the rate of sedimentation are likely to be associated with elevated levels of nutrients when compared to pristine sites (Airoldi 2003), especially if sediments are from agricultural origins (Hessen et al. 1997). Therefore, when considering the effects that sedimentation may have on the structure of rocky intertidal communities, there is a need to examine the effects of elevated nutrient levels on communities and whether this is affected by the sediment environment.

Increased nutrient levels in coastal waters are sourced largely by sediments washed from highly fertilised, agricultural land (Thompson et al. 2002). Nutrient loadings in coastal waters may be exacerbated by climate change because predicted increases in rainfall will increase leaching of organic nitrogen (Hessen et al. 1997) and increase runoff. To manage the impacts of increased nutrient availability in coastal waters there is a need to know both the geographical scale over which nutrients vary and their effects (Russell et al. 2005) as well as the community's resilience if the impacts are removed (Kraufvelin et al. 2006). The effects of eutrophication on aquatic ecosystems have been explored, but because effects in rocky shores have been less pronounced (Nielsen 2001) they have received significantly less attention (Vidal et al. 1999). Rocky shores are perceived to have a reduced sensitivity to nutrient enrichment because of higher rates of water exchange, physical exposure and diverse community structure (Bokn et al. 2003).

Research into the interactions between grazers and algae in areas with increased nutrient concentrations has found that there is a combination of factors that control their relationship. Coasts with low grazer abundance may be most affected by nutrient addition because of a lack of top-down control to remove opportunistic algae (Russell & Connell 2005). Subtidal experiments assessing the effects of grazers on nutrient and algal abundance have found the removal of algal biomass by grazers is greater with elevated nutrient levels compared to non-elevated levels (Russell & Connell 2005). Experiments in the Baltic found that the effects depended on the original nutrient state of the ecosystem, the algal life history strategies of the community and the season (Lotze et al. 2001). Grazing gastropods also have

the potential to alter the sediment environment either by bulldozing sediment or by grazing algae that bind the sediments (Bertness 1984).

Long-term enrichment by inorganic nitrogen and potassium have been shown to cause a rapid response of ephemeral algae, but little or no response in filamentous red and perennial brown algae (Bokn et al. 2003). However, this response did not alter the biomass balance of the communities, possibly due to grazing, suggesting that perennial brown algae can resist an increase in nutrient loading (Bokn et al. 2003). In this chapter I test the hypothesis that altering the sediment load, nutrient levels and grazer abundance in an intertidal community affects community composition, especially the relative abundance of ephemeral green algae.

4.2. Methods

4.2.1 Experimental design

Field experiments were established in December 2008 to test the interaction between the sediment environment, nutrient load and grazers. Nutrient treatments were either the addition of nutrient bags (+Nutrient), addition of control bags of plastic beads mimicking the nutrient pellets inside the nutrient bags (+Beads), or control plots with no beads (=Nurtient). Grazer treatments were grazer exclusions (-Grazer) and inclusions (+Grazer) and controls (=Grazer) without cages. Sediment manipulation was either the removal (-Sediment) or maintenance of natural sediment loads (+Sediment) (Fig 4.1). The design is not completely orthogonal, with the control nutrient treatment only being applied to the control grazing treatment due to time and space constraints (Fig 4.1). Three replicates of each treatment (total 42 plots, 10x10 cm^2) were placed out adjacent to the high southern site used in Chapter 2 on the southern side of the Kaikoura peninsula.

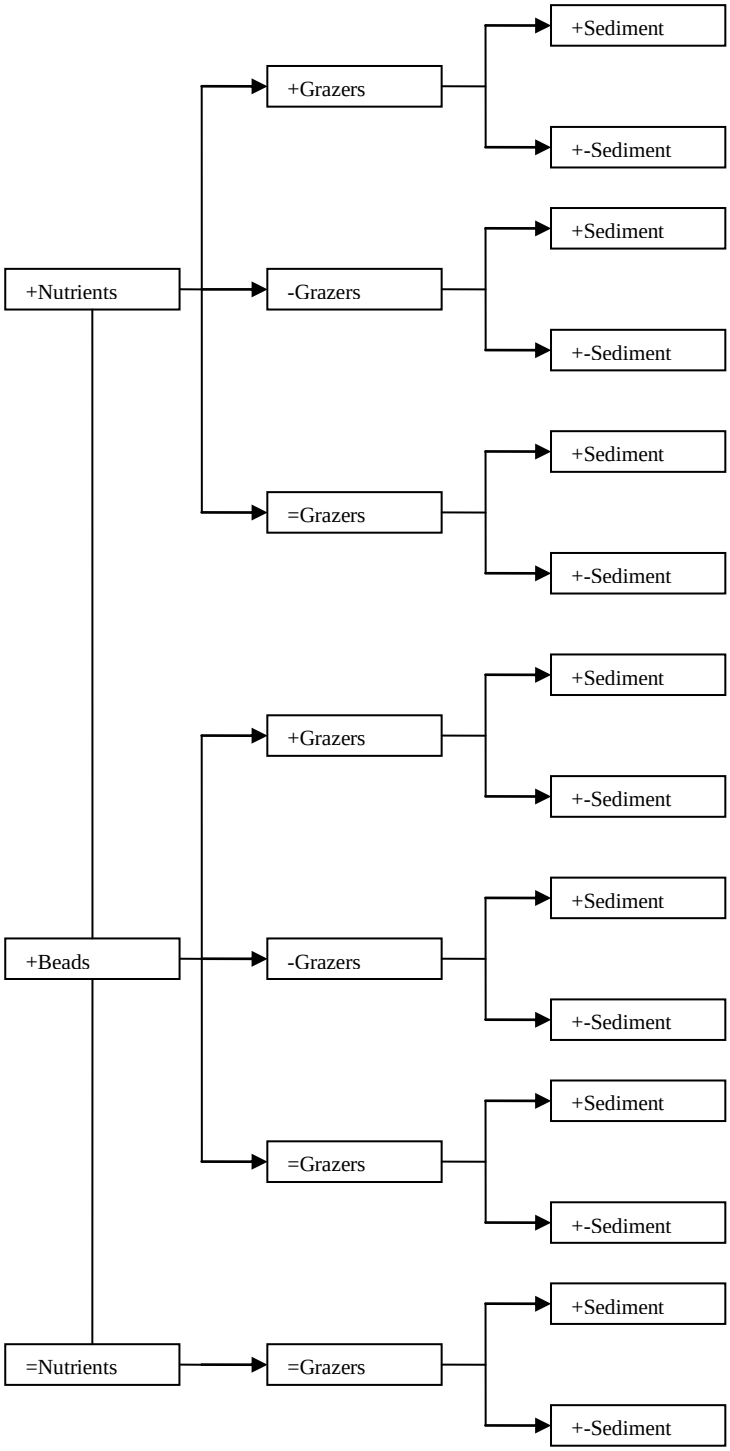


Figure 4.1 Experimental design showing three levels of nutrient manipulation, three grazer manipulations and two levels of sediment manipulation.

Grazer inclusions and exclusions were achieved using stainless steel mesh fences with a 2mm hole diameter. The fences were 10 x 10 cm and 4 cm high, with a 2 cm lip at the top, covered with vexar mesh. Grazer additions consisted of two similar sized *Turbo smaragdus* and two *Melagraphia aethiops*, the dominant macro-gastropods on the Kaikoura peninsula (Lilley 2004).

The addition of nutrients was in the form of Osmocote™ fertilizer (Scott, Australia). These are pellets (2–5 mm diameter), with a combination of essential plant nutrients (Table 4.1), coated with a semi-permeable resin to allow for gradual release.

Two 150g loads of fertiliser contained within 15x15cm nylon mesh bags (mesh size 1mm^2) were attached beside each +Nutrient plot and were held in place against the substratum by a covering of vexar mesh (Fig 4.2). Nutrient bags were replaced after 6 weeks, as fertiliser pellets would have released most of the nutrients by then (Worm et al. 2000). Two 150g bags of plastic pellets of similar diameter to the fertilseer were used in +Bead plots. The bags were removed after 6 weeks and washed to remove accumulated sediment and epiphytic algae, and were then returned to treatments. Control treatments consisted of marked plots with no cages and no nutrient or plastic pellet bags.

In the sediment removal treatments (-Sediment), sediment was removed sporadically inside the plots and in the surrounding area, totalling about 20x20cm. Sediment was gently washed out using buckets of water. All treatments were monitored for species abundances and physical characteristics before treatment application and again immediately after if sediment removal was done. All plots were monitored at approximately one and two months. For algae, sessile invertebrates, bare space and sediment, percent cover was estimated. Mobile invertebrates were counted. Sediment depth was measured and grain size estimated (silt, sand and gravel) before treatment application. The experiment ran from December 2008 until February 2009, to assess the short-term community response to nutrient additions.

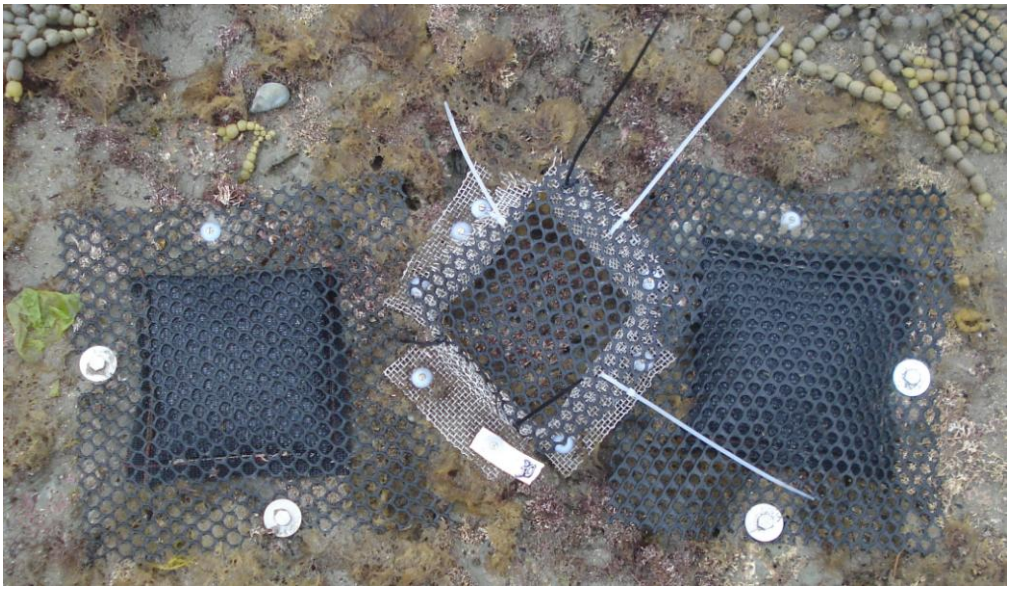


Figure 4.2 Photograph of experimental setup, cage in the centre, with adjacent nutrient bags covered with Vexar mesh.

Table 4.1 Nutrient composition of Osmocote fertilizer (from manufacturer's information).

Nutrient	Percent	Nutrient	Percent
Nitrogen	16	Copper	0.05
Phosphorus	3.5	Iron	0.4
Potassium	3.5	Manganese	0.06
Sulphur	2.4	Molybdenum	0.02
Magnesium	1.2	Zinc	0.015
Boron	0.02	Organic Resin coating	8

4.2.2 Data analysis

The experimental design was not balanced so interaction terms could be examined only by excluding the +Bead treatment. Because this treatment showed no significant interactions between any combination of grazers, nutrients or sediment, a 3-way ANOVA excluding the interaction terms was used in the analysis. Treatment responses were measured as a percentage change from initial monitoring (Time-0) until final monitoring (Time-2) (December 2008-February 2009). All analysis was done using *Statistica* 7.1.

4.3. Results

4.3.1 Experimental results

Despite the range of experimental manipulations, the changes in community structure over the experiment were largely independent of treatments. Ephemeral algae (*Ulva* spp. and *Colpomenia* spp.) had a variable response to the treatments (Fig 4.3), with grazers having the only significant effect (Table 4.2). The =grazer treatments generally showed a greater increase in ephemeral algal cover than in the other grazer manipulations (Tukey HSD, $p<0.05$). Despite there being no consistent effect of nutrient addition on ephemeral green algae, it did recruit onto the nutrient bags and in surrounding areas (Fig 4.4).

Algal diversity showed variable responses between treatments (Fig 4.5), with none of the manipulated factors producing a significant effect (Table 4.3). Eight algal species were found during the study, pooled across all treatments, but the maximum percent changes represented an average increase of only 1 species. Mean diversity before treatment application in December 2008 was 3.0 algal species per plot (± 0.41 SE) and atthe end of the experiment 2.9 species per plot (± 0.02 SE). The increases in species diversity were most often the addition of *Ulva* spp. to one or all of the replicates. Decreases in mean algal diversity were mainly due to the seasonal die-back of *Polysiphonia decipiens*. Average covering of *Polysiphonia decipiens* decreased from 54.8% (± 5.1 SE) in December 2008 to 18.6% (± 3.9

SE) in February 2009. *Corallina officinalis* increased from 9.1% (± 1.1 SE) in December 2008 to 22.5% (± 4.0 SE) in February 2009, mainly due to the die-off of *P. decipiens.* There were no significant treatment effects on the total cover of algal species (Table 4.4) but, in general, algal cover decreased over the experiment (Fig 4.6).

By the end of the experiment there were significantly more micro-gastropods (*Zeacumantus subcarinatus* and *Eatonella* spp.) in the natural sediment treatment than in the sediment removal treatments (Fig 4.7) (Tukey HSD, p=0.002). There were no significant effects of either macro-grazer addition or removal or the nutrient loading on the density of micro-grastropods (Table 4.5).

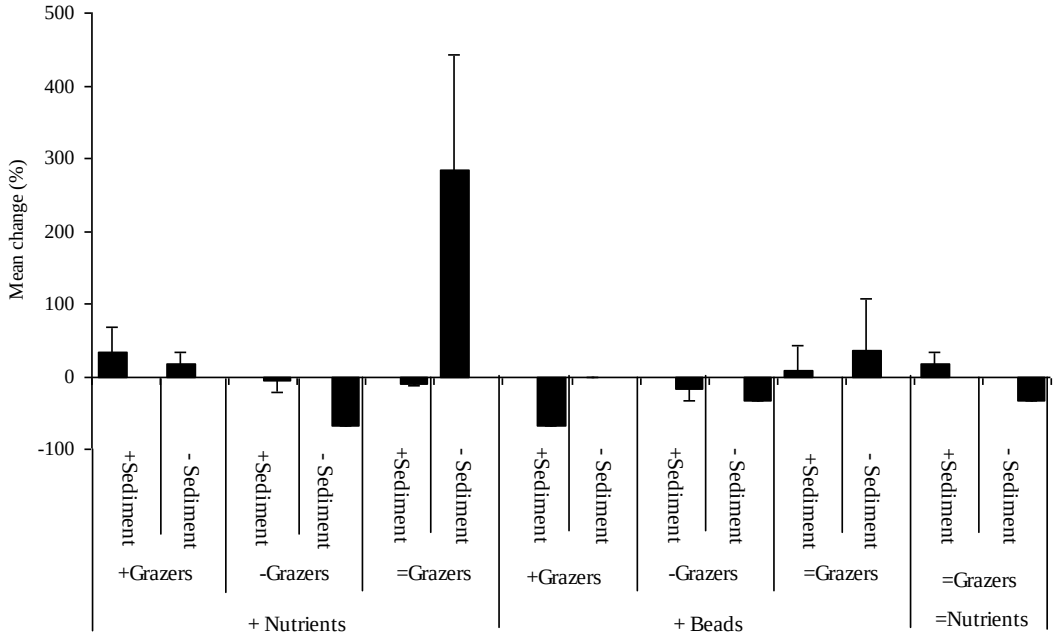


Figure 4.3 Mean change (%) in ephemeral algae cover (+SE) from before treatment application (December 2008) to the end of the experiment (February 2008).

Table 4.2 Three-way ANOVA on the effect of nutrients, grazers and sediment had on the percentage change in ephemeral algae cover, over the course of the experiment (December 2009-Febuary 2008)

Effect	Df	MS	SS	F	p
Grazers	2	78933.8	39466.9	3.551	**0.039**
Nutrients	2	56589.7	28294.8	2.546	0.092
Sediment	1	12862.5	12862.5	1.157	0.289
Error	36	400082.9	11113.4		

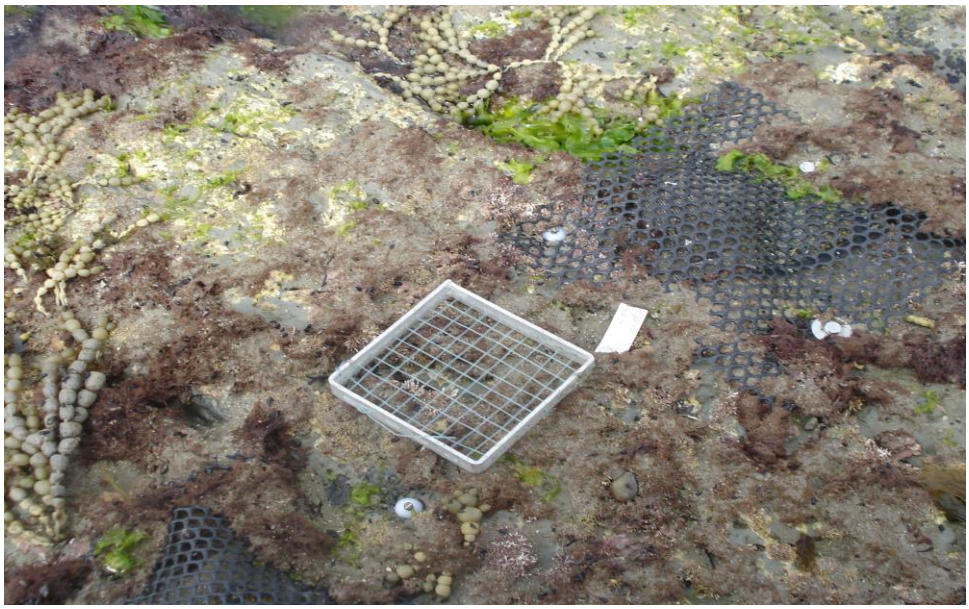


Figure 4.4 +Nutrient, =Grazers and +Sediment treatment showing increased *Ulva* spp. recruitment onto mesh bags and surrounding bare rock compared to those inside the marked plot.

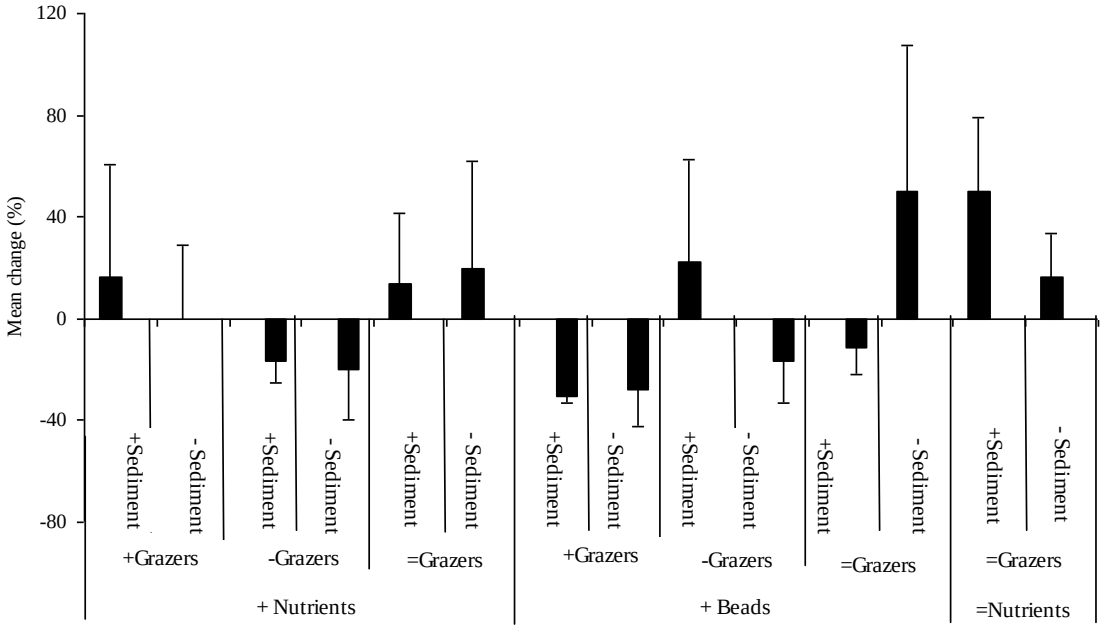


Figure 4.5 Mean change (%) in algal diversity (+SE) from before treatment application (December 2008) to end of the experiment (February 2008).

Table 4.3 Three-way ANOVA on the effect of nutrients, grazers and sediment had on the percentage change in mean algal diversity, over the course of the experiment (December 2008-Febuary 2009)

Effect	Df	MS	SS	F	p
Grazers	2	6000.5	3000.2	1.204	0.312
Nutrients	2	1109.6	554.8	0.223	0.802
Sediment	1	105.8	105.8	0.042	0.838
Error	36	89734.1	2492.6		

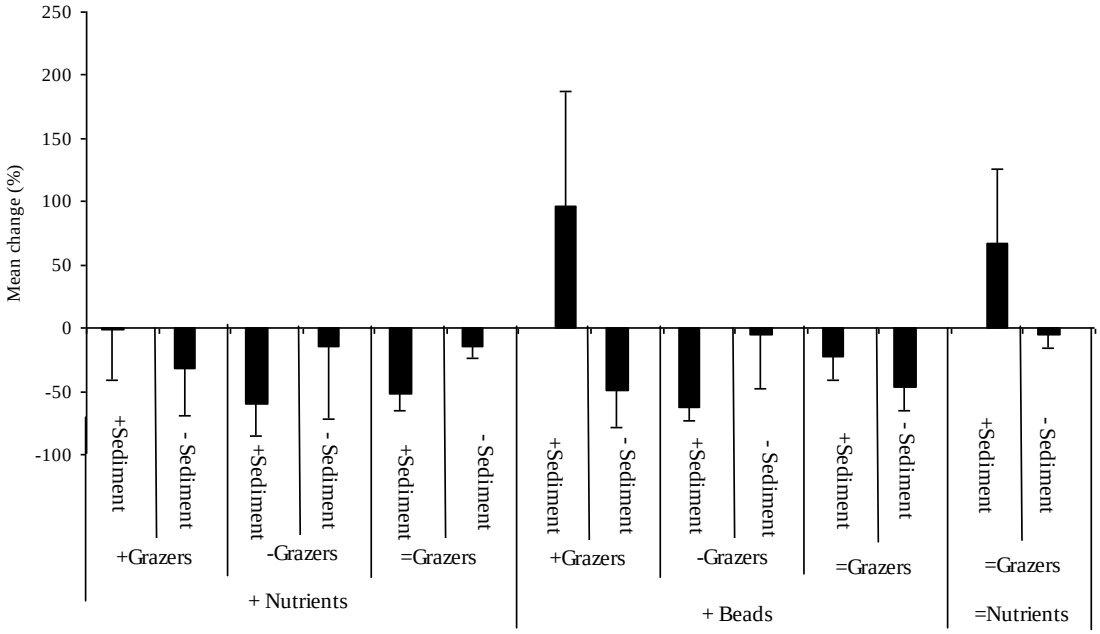


Figure 4.6 Mean change (%) in the cover of algae (+SE) from before treatment application (December 2008) to end of the experiment (February 2008).

Table 4.4 Three-way ANOVA on the effect of nutrients, grazers and sediment have on the percentage change in total algae cover, over the course of the experiment (December 2008-Febouary 2009)

Effect	Df	MS	SS	F	p
Grazers	2	11683.3	5841.6	1.129	0.334
Nutients	2	18696.2	9348.1	1.807	0.179
Sediment	1	4042.2	4042.2	0.782	0.383
Error	36	186197.4	5172.2		

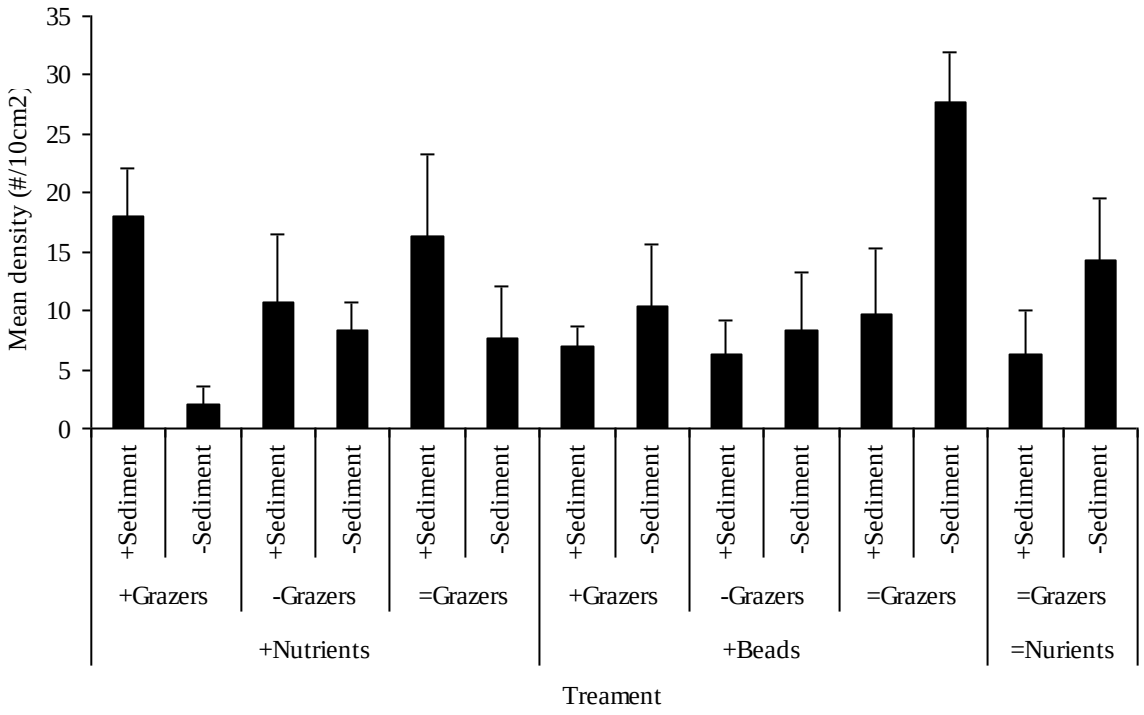


Figure 4.7 Mean density (+SE) of micro-garazers at the end of the experiment (February 2009).

Table 4.5 Three-way ANOVA on the effect of nutrients, grazers and sediment on the density of micro-grazers February 2009.

Effect	Df	MS	SS	F	p
Grazers	2	628.6	314.3	2.636	0.076
Nutrients	2	43.9	22.0	0.184	0.832
Sediment	1	1188.6	1188.7	9.971	0.002
Error	36	14305.3	119.2		

4.4. Discussion

The results of this experiment indicate that rocky shore communities are resilient to short term pulse increases in nutrients. Only one nutrient addition treatment showed any significant response in ephemeral algae. It was expected that the addition of nutrients, with the exclusion of grazers and the additional disturbance of sediment removal, would produce a strong from ephemeral algae, especially *Ulva* spp.. Ephemeral algae were expected to flourish with release from the top-down control from grazers and the bottom-up control of nutrient limitation (Bokn et al. 2003), but this was not the case here.

There are three proposed mechanisms explaining the lack of ephemeral algae response to nutrient addition, based on previous research: 1) strong competition for space and light due to dense communities 2) top down control by herbivores 3) physical disturbance by wave action exporting algal matter (Bokn et al. 2003). Although the filamentous alga *P. decipiens*

did die-off over summer, consistent with previous reports its on abundance (Adams 1991), this revealed a primary covering of *C. officinalis*. Thus for the study period, free primary space was effectively limited and any recruiting algae would have had difficulty establishing except as epiphytes. Ephemeral algae are characterised by their ability to quickly colonise disturbed areas, but also for their poor competitive ability (Molina-Montenegro et al. 2005). Therefore, it is likely that for ephemeral algae to respond to changes in to the nutrient environment, there is a need for it to be coupled to a disturbance event that removes algal biomass and creates primary space. The nutrient bags and Vexar mesh provided an artificial substratum and after 6 weeks, when the nutrient bags were exchanged, *Ulva* spp. had recruited onto these surfaces.

Top-down control of ephemeral algae by grazers was not evident during this study, with macro-grazer exclusion treatments showing a decrease in the cover of ephemeral algae. Previous research has suggested that grazers preferentially graze ephemeral algae, and can maintain lowered cover compared to grazer exclusions (Korpinen et al. 2007). However, grazers have also been shown to facilitate the early growth of macro-algae becase spores, particularly of ephemeral algae, can be resistant to digestion by invertebrates and can survive to grow in faecal pallets (Amsler et al. 1992).

Wave action may have limited the response of ephemeral algae to nutrient addition by removing delicate recruits. Fragments of *Ulva* spp. were often found caught in and around the cages, but it was not possible to tell if this material washed into or out of the plot. Another important factor that may have limited the response of ephemeral algae to nutrient addition is that this experiment was done during summer when heat and desiccation stress is at its maximum. It is possible, therefore, that a response of ephemeral algae was muted due to burn-off equalling the increased biomass production where bare space was available.

The dominant alga in the experimental plots at the outset of the experiment was the filamentous red alga *P. decipiens*. This species died-off over summer across all treatments, so it was impossible to detect either a grazing or nutrient effect. The only conclusion that can be drawn is manipulations of grazers and nutrient additions did not override natural seasonal fluctuations in abundance. Results from mesocosm experiments suggest that nutrient enrichment of an algal community does not enhance the growth of filamentous red algae (Bokn et al. 2003). However, subtidal experiments along the south Australian coastline showed that nutrient enrichment resulted in a six times greater increase in the percentage cover of filamentous algae the than the to addition of sediments or nutrient-enriched sediments (Gorgula & Connell 2004). These subtidal experiments suggest that coastal

eutrophication may magnify the effects of sedimentation by hastening the rate of expansion of turf-forming algae, thereby providing more surface area for sediment entrapment (Gorgula & Connell 2004).

The food preferences of grazers are thought to change with nutrient enrichment (Russell & Connell 2005). In the Baltic Sea, fucoid recruitment densities did not alter with grazer exclusion or inclusion under ambient nutrient levels, but there was a negative response at high nutrient levels as grazers switched to feeding on *Fucus vesiculosus* recruits when other algae were overgrown by unpalatable brown filaments (Korpinen & Jormalainen 2008). This allowed the expansion of ephemeral brown algae.

Grazers are also thought to counter-balance the effects of increased nutrients, by eating ephemeral algae (Russell & Connell 2005). The micro-grazers in this experiment did not respond to nutrient enrichment but they did decrease in abundance due to sediment removal. This may be an effect of physical sediment removal or a preference for sedimented areas due to moisture retention. Because sediment removal occurred at least a week prior to each monitoring, it is likely that within that time micrograzers were able to return to natural densities, suggesting that this was a response to sediment removal. The most common micro-gastropod in this experiment, *Zeacumantus subcarinatus*, is common on both rocky and sandy substrata (Martorelli et al. 2008) so its abundance was not expected to vary with sediment level. Possibly local adaptation has occurred to the current sediment environment, explaining their preference for the natural sediment environment. The removal of sediment could have also removed microalgae, the main food source for micro-gastropods (Underwood 1984).

Several factors are implicated for a shift in community structure to occur: 1) a large-scale disturbance event that removes the encrusting coralline turfs and creates bare space for ephemeral algae to recruit onto, like the response seen in the clearance treatments in Chapter 2; 2) recruitment of the ephemeral algae in a species-poor community would respond to nutrient enrichment, inhibit recruitment of species in the original community, causing the establishment of a new community (Crowe et al. 2000); and 3) nutrient enrichment needs to occur over an extended period. Long term mesocosm experiments have shown that *Ulva* spp. showed a slight effect after a few months of nutrient addition but there was no dramatic change on community structure over the first 3 years of nutrient additions (Bokn et al. 2003). During the fifth year there was a natural die-off of perennial fucoid algae and communities became dominated by *Ulva* spp. The recovery of communities after the removal of nutrient impact was rapid, with community structure returning to within normal variability after 2

years, showing the high degree of resilience rocky shore communities to nutrient disturbance (Kraufvelin et al. 2006).

4.4.1 Summary

The results of this study suggest that rocky shore communities lend support to the argument that they are resilient to short term pulse fluctuations in nutrient levels. Under natural levels of grazing there was a positive change in ephemeral algal cover, unexpected at the outset of the experiment. Sediment removal did not affect the overall abundance of algae, but did alter the abundance of micro-grazers, which were able to move in and out off all treatments.

Chapter 5. General Discussion

Although sedimentation is considered a threat to rocky intertidal community structure, mechanisms of how sediments affect individual species and communities as a whole have often been explored with observational studies rather than by experimentation. In this thesis, the effects of sedimentation on mid–shore, algal-dominated communities were tested through a series of structured observations and experiments. There was a focus on the effects of sedimentation on habitat-dominating fucoid algae, and in particular, their interactions with benthic algal turfs in combination with disturbances. I found that sediments accumulated in algae with particular morphological and physiological traits, that this had direct effects on community structure and secondary effects through recruitment failure of fucoids. Furthermore, sediments interacted with physical disturbance to alter early successional communities, but had little interactive effect with elevated nutrients on algal communities. This study differs from the majority of studies on sediment and rocky shore communities by having direct measures of sedimentation, experimental manipulations and lab experiments with quantifiable levels of sedimentation (c.f., Airoldi 2003).

My study has extended the large body of previous subtidal work from the Mediterranean (Airoldi et al. 1996, Airoldi & Cinelli 1997, Airoldi 1998, Airoldi & Virgilio 1998, Airoldi 2000), Baltic (Vogt & Schramm 1991, Pedersen & Snoeijs 2001, Isæus et al. 2004, Eriksson & Johansson 2005) and South Australian (Irving & Connell 2002, Connell 2005) coasts, where sedimentation has been shown to be a driving factor behind shifts in species' distributions and dramatic alterations to community structure.

5.1. Kaikoura sediment environment

Sediment accumulation around the Kaikoura peninsula had several differences compared to other temperate reef ecosystems. In general, sediment accumulated gradually over the year except for a single large pulse at one site during an extreme weather event. Sedimentation rates in many other reef systems are strongly influenced by anthropogenic sources to such an extent that sedimentation rates are increased year-round compared to historical measures (Airoldi 2003). In these situations, sediment can be considered a long-term press disturbance, resulting in new, possibly stable-state communities. Sediment sources in New Zealand are largely derived from natural erosion processes, which may be elevated by historical land use changes and current agricultural practices.

New Zealand has a relatively high natural rate of sedimentation, especially along the east coast of the South Island (Griffiths & Glasby 1985). Natural sedimentation rates in this study far exceed those reported in previous shallow subtidal research (Table 5.1), but this can be explained partly by the different physical conditions between intertidal and subtidal zones. However, New Zealand has not generally had large increases in sedimentation due to coastal construction (except for some areas around large cities), and there is little toxic chemical loading of sediments due to runoff seen in other developed nations (Thompson et al. 2002).

One of the most cited examples where anthropogenic increases in sedimentation have influenced algal communities is in the Baltic Sea, where there has been an upward shift in the vertical distribution of *Fucus* (Kautsky et al. 1986) and an overall decline in *Fucus* due to coastal sedimentation and eutrophication (Vogt & Schramm 1991). Another sediment-influenced coast that has been used for numerous studies is along the Mediterranean, where sedimentation rates are moderately large compared to other shallow coastal areas (Airoldi et al. 1996), with average sedimentation rates of $32.5 gm^{-2}d^{-1}$ (Airoldi & Virgilio 1998). However, this is significantly lower than the values in my study. Using the same conversions based on the collection area of my sediment traps, deposition around the Kaikoura peninsula ranged from 2314 to $43290 gm^{2}d^{-1}$. Sediment traps in my study were closer to the substratum than in subtidal studies, and therefore would have contained re-suspended sediments as well as flux from the water column. In many ways, this is a more realistic measure of the potential impact of sedimentation on benthic communities because it assays the immediate environment that the communities must cope with. Waves redistribute sediment more in the intertidal environment than in subtidal locations. This will further elevate sediment flux (Gaylord 1999). Despite these large differences in the rate of sedimentation, there are similarities between this study and the large number of studies undertaken in the shallow subtidal zone of the Mediterranean Sea. Principally, rates of sediment deposition vary greatly on a scale of metres (Airoldi & Virgilio 1998) and there is significant temporal variation in sediment deposition (Airoldi et al. 1996). This is particularly true of sediment deposition on the northern side of the Kaikoura peninsula.

Large fluctuations in sediment cover are not always attributable to anthropogenic impacts. For example, D'Antonio (1986) found that at one site on the Oregon coast (Strawberry Hill) sand accumulates as wave steepness declines during Spring, with major burials of the reef occurring in the late summer. In autumn, accumulated sand is moved seaward by wave action during storms. However, another site (Boiler Bay) had a constant low covering of coarse sand year-round. Despite the seemingly less stressful impact of

sedimentation on the Kaikoura peninsula when compared to other temperate reefs, results from my study showed significant responses of intertidal communities to a varying sediment environment throughout the year.

Table 5.1 Sedimentation rates measured from sediment traps in a range of shallow subtidal locations (adapted from (Airoldi et al. 1996).

Location	Bottom depth (m)	Height of traps of the bottom (m)	Deposition ($gm^{-2}d^{-1}$)
Cape Cod Bay, Massachusetts, USA	12	0.2	~ 18
Discovery Bay, Jamaica	4	1	5 - 11
Banyuls sur Mer, France	32.5	-	10.4 - 82.5
Kiel Bight. Baltic Sea	20	2	1.7 - 5
Kie1 Bight, Baltic Sea	20	2	~ 0.1 - 349
St Thomas, USVI	3-5	0.1	8 - 58
Puerto Rico	4	0.1	96
Paraggi Bay, Italy	24	8	11.9 - 129.7
Academy Bay, Galapagos	<2	0.5	100 - 550
Western Baltic Sea	10.5-16	1	0.2 - 13.3
Gulf of Trieste, Italy	17	1	10 - 108
Northern Adriatic, Italy	32-37	2	2.1 - 41.3
Ligurian Sea, Italy	14.5	0.5	3.1 - 52.4
Kaikoura peninsula, New Zealand	0	0.3	~2314 - 43290

5.2. Effects of sediment on rocky shore community structure

Examining communities as a whole, there were clear differences in diversity between sites at the outset of the experiment. These differences were partially explained by the gradient of sedimentation, especially on the northern side of the peninsula. In the northwest Mediterranean, experimental increases in sedimentation enhanced similarities between algal communities on vertical and horizontal substrata, overriding the influence of inclination on beta (between site) diversity (Balata et al. 2007a). Subtidal experiments in South Australia found that accumulation of sediment removed micro-topographic differences between simple and complex experimental surfaces (Irving & Connell 2002). Complex micro-topography is thought to enhance the attachment of spores by increasing turbulence and creating pockets of slow water flow (Amsler et al. 1992). In Kaikoura, all plots were established on horizontal surfaces, but sediment did reduce habitat complexity by clogging cracks, crevices and depressions in the rock surfaces. This may explain the reduced species diversity and abundances at the high northern site compared to other sites on the northern side of the peninsula (c.f., Irving & Connell 2002, Balata et al. 2007a). If sedimentation was to increase around the Kaikoura peninsula, it is likely that assemblages on the northern side of the peninsula would converge to have similar species composition and abundances to that at the

high sediment site, with an associated loss of species diversity. The loss of these species may produce a loss of functional diversity (Balata et al. 2007a) that could result in alterations to the rate of productivity and resistance to secondary disturbances, while also increasing the chance of biological invasions (Chapin et al. 2000).

Sediment-dominated communities favour species with tough thalli, species that bind and trap sediments (e.g. *Polysiphonia* spp.) and ephemeral species that can colonise unstable sediments (e.g. *Ulva* spp.). These species are present in low sediment environments also, but at lower abundances. This pattern of abundance suggests that these species are not sediment-dependent; rather a high sediment environment increases their survival or at least diminishes the survival of other species. Along the Oregon coast, the red alga *Rhodomela larix* occurs in sediment-free and sediment-influenced rocky shores. However, like many of the species in my study, it is more abundant where sands are present (D'Antonio 1986). Once established, *R. larix* is resistant to sand disturbance, and D'Antonio (1986) listed four possible benefits that sand may confer to *R. larix*:

1) refuge from grazers;
2) elimination of epiphytes;
3) removal of algal competitors that are intolerant of sediment;
4) prevention or slowing of recruitment of sexual species (*R. larix* grows through lateral propagation).

The intertidal zone in Kaikoura is mostly devoid of the large predators seen on other temperate rocky reefs (Lilley 2004), therefore the first of D'Antonio's (1986) suggested benefits is unlikely to be supported. Epiphytic cover of fine microscopic algae was not examined in this study, although none were obvious, but studies of diatoms and other such algae elsewhere have shown epiphytes to have a negative effect on the growth and survival of macroalgae (Worm & Sommer 2000). The final two suggested benefits from D'Antonio's (1986) study are more likely to explain the patterns in species diversity and abundance seen in my study. Sediment has been shown to inhibit settlement of the dominant intertidal fucoid species at Kaikoura, *H. banksii* and *C. torulosa* and numerous algal species including laminarians (Devinny & Volse 1978), fucoids (Chapman & Fletcher 2002, Isæus et al. 2004, Schiel et al. 2006, Irving et al. 2009), and probably other spore-producing algae (Eriksson & Johansson 2005). Furthermore, many of the species that occurred at sediment-dominated sites around the Kaikoura peninsula grew mainly through either asexual reproduction or vegetative propagation (e.g. *C. officinalis*) which is in support of D'Antonio's (1986) fourth benefit and other experiments (Eriksson & Johansson 2005).

C. officinalis has been reported to be resistant to the effects of sedimentation (Stewart 1989, Kelaher et al. 2001). This was confirmed at Kaikoura by its resilience to extended burial at the high northern site during the storm events. Its resistance to sedimentation and ability to bind and stabilise sediment indicate that turfing algae play an important role in structuring communities via alterations to the sediment environment.

One portion of the fauna that was not extensively examined in this study was the meio- and macrofauna associated with turfing communities. Huff and Jarett (2007) found that experimental additions of sand to coralline turf communities had immediate and sustained effects on meio- and macrofauna. There was a rapid exodus of sand-intolerant animals (e.g. amphipods and ostracods) and a more gradual increase in sand-tolerant gastropods. This was found to be a response to sediment clogging the coralline turf and removing spatial niche and refuge from predators (Dean & Connell 1987). These differences have the potential to propagate up the food web because the meiofauna that decreased in abundance with sand deposition are important food sources for fish and invertebrates, and also play an important role in making detritus available to macro-consumers (Huff & Jarett 2007).

5.2.1 Fucoids and Sediment

Although sediments are likely to affect all species in rocky intertidal communities to some extent, the direct effect of sediment on the recruitment and subsequent survival of fucoid algae is of most concern. Fucoid algae not only make up a significant proportion of rocky shore biomass, but they also provide ecosystem goods and services for other algae and animals (Sensu Jones et al. 1997). Therefore, any loss of fucoid canopy can cause dramatic alterations to communities. These effects are often predictable and rapid (Reed & Foster 1984, Santelices & Ojeda 1984, Melville & Connell 2001), via alteration to positive and negative interactions. In the Kaikoura region, the loss of fucoid canopies in the mid-intertidal zone causes abrupt and long-lasting effects on understory species and a significant decline in diversity (Lilley & Schiel 2006, Schiel & Lilley 2007). My experiments showed that on the southern side of the peninsula, where fine silts dominate, algal diversity is lower due to reduced cover of canopy forming algae. Canopy-forming algae may have been inhibited because of the spatial dominance of filamentous *Polysiphonia* spp. and the rapid recruitment of *Ulva* spp. into any bare space; these are species that do well in high sediment/silty environments. Replacement of canopy algae with turfing and filamentous algae has been reported on numerous rocky shores worldwide as a response to increases in sediment load. In this study, using the natural gradient of sedimentation on the northern side of the peninsula, it

was clear that with an increase in sediment flux and standing stock of sediment there was a decrease in fucoid cover.

The influence of sediment on the successful recruitment and subsequent survival of fucoid algae was highlighted in experiments in Chapters 2 and 3. Although the amount of sediment used in the settlement experiments (Chapter 3) was lower than those found in turf core samples (Chapter 2) and values reported in the literature (Irving et al. 2009), it served the purpose of covering the primary substratum in a manner similar to that of the total clearance treatments (Chapter 2). Attachment to the primary substratum was inhibited by sediment, but the effect was species-specific with the "stickier" *C. torulosa* having a lower probability of reaching the substratum than *H. banksii* (cf. Taylor & Schiel 2003). I did not examine the survival of attached embryos if sediment cover was extended beyond 48 hours. However, it is predicted that there would be a high rate of mortality of attached embryos if they are covered by sediment. Previous studies have shown that prolonged burial by sediment alters the light environment and in some cases results in abrasion. However, some fucoid embryos can remain alive for over six weeks with no light, so burial may only affect growth rates (Irving et al. 2009). Sediment may cause mortality of attached embryos by limiting micro-scale water movements, thus creating a barrier to diffusion of essential nutrients and metabolic wastes (Chapman & Fletcher 2002). Because my lab experiment was carried out in the absence of water motion, diffusion barriers or scour could not be responsible for any of the observed effects, but they may play an important role in the natural world. I also assumed that embryos attached directly to sediments would be washed away and would have little chance of attaching to primary substratum.

5.3. Mechanisms of sediment disturbance

Sediment scour can influence attachment (Devinny & Volse 1978, D'Antonio 1986) and survival of recent algal recruits. *H. banksii* recruited mostly into patches of bare space in field experiments and thus was more likely to be affected by sediment scour than species that recruit into turf assemblages. At the intermediate northern site, however, the dense patches of *H. banksii* recruits seemed to act similarly to coralline turf in trapping sediments, reducing abrasion and maintaining a moist environment during aerial exposure. It is possible that nutrient exchange could be inhibited in these dense patches, but as the tops of the recruits were uncovered this is unlikely. Increased scour is important when sediment levels exceeded that of the turf which binds and stabilise it. This only occurred at the high northern site during

the August storms and subsequent burial. The high northern site also had the highest proportion of sand-sized sediments, which are more abrasive than silts (Airoldi 2003), reducing algal diversity to only those species resistant to abrasion i.e. those with tough thalli (e.g., *C. officinalis*).

Algal biomass and species composition were affected greatly at one site after complete burial during an extreme storm event. Experimental burials in the Gulf of California found that with 20 days of burial there was a catastrophic loss of all algal species due to smothering preventing photosynthesis and nutrient exchange (Yanez et al. 2008). This differs from results seen in my study. In my study there was no reduction in cover of *C. officinalis,* as the tough calcareous thalli and low photosynthetic requirements made them resistant to the negative effects of burial (Hay 1981). Adult *H. banksii* survived burial because their long strings of bladders were never completely buried. The greatest effects of burial on the community resulted from blooms of ephemeral algae, with increased cover of *Ceramium* sp. and *Ulva* spp., rather than the loss of either biomass or diversity.

The silts that dominated the southern side of the peninsula because of constant riverine input are more likely to remain in suspension. In other areas such as the Baltic coast, alterations of the light environment from suspended matter have been shown to be responsible for the upward shift of subtidal algal communities (Pedersen & Snoeijs 2001). This is unlikely to occur in the intertidal zone, but may act to slow growth rates due to suboptimal rates of photosynthesis.

Sediment-dominated shores favour ephemeral species that can inhibit and slow the recover of other algal species after a disturbance event (Kim 1997, Foster et al. 2003). The rapid accumulation of biomass exhibited by ephemeral species such as *Ulva* spp. can pre-empt the recruitment of other algae by quickly monopolising bare space (Molina-Montenegro et al. 2005). Furthermore, blooms of *Ulva* spp. occurred during early summer, the period of maximum reproductive output for most New Zealand fucoid species (Taylor & Schiel 2003, Schiel 2004), further exacerbating the inhibitory effect. *H. banksii* is reproductively active year round and is more likely to be able to recover outside the periods of *Ulva* blooms, but since survival is density-dependent and reproductive output is lower during these periods, recovery of a complete canopy can be slowed (Schiel & Foster 2006).

5.4. Sedimentation interacting with other disturbances

Increases in physical disturbance are likely to interact with sedimentation to affect the *Corallina* communities that stabilise sediments on the benthos. The slow rate of recovery of *Corallina* spp. makes space available for fucoid recruitment. However, as described above, under sediment-dominated conditions total clearances became dominated by ephemeral algae. This, combined with a thin layer of sediment, will inhibit the recruitment of fucoid algae into bare space. Experiments in Argentina have also found a negative relationship between the cover of *C. officinalis* and cover of the ephemeral green alga *Ulva lactuca* (Daleo et al. 2006).

Recovery in plots that suffered loss during the reduction in turf height was faster because of the lateral encroachment of remaining branches. This highlights the effect of disturbance magnitude on the recovery of algal communities (Sousa 1984, Benedetti-Cecchi & Cinelli 1994). Experiments in the low tidal zone in the Mediterranean Sea found that the recovery rate of *Corallina elongata* patches was affected by the size and timing of the clearance. However, unlike my study, smaller clearances had a lower percentage cover of *C. elongata* as lateral growth appeared to have little relevance to survival. Rather, recovery was from the recruitment of spores or regeneration from persistent basal crusts (Benedetti-Cecchi & Cinelli 1994). Clearances in the intertidal zone in New South Wales, Australia took between 6-18 months to converge, with surrounding communities with *Corallina* showing quick recovery on most shores (Chapman & Underwood 1998).

Partial removal of biomass due to a small-scale physical disturbance such as sand abrasion or wave action is also important in small-scale differences in intertidal communites. Subtidal experiments on the Mediterranean coast found that when sedimentation rates were greater than 200g $m^{-2}d^{-1}$ there was a decrease in the biomass of the filamentous turfing alga *P. setacea* due to erect axes being removed by scour. The loss of horizontal branches would have decreased the volume of sediment held within the turf, increasing at least temporarily the suspended load of sediment possibly increasing turbidity and scour depending on the size composition of the sediment. Small scale disturbances do not have the same magnitude of effects as larger events, but their greater frequency and occurrence over larger spatial scales contribute to the patchiness seen in macroalgae communities (Schiel & Foster 2006).

Effects of nutrient additions have been studied extensively in laboratory and mesocosm experiments (Worm et al. 2000, Bokn et al. 2003, Kraufvelin et al. 2006, Kraufvelin 2007). Results suggest that increased nutrients favour ephemeral algal species at the expense of canopy-forming macroalgae, although there is likely to be a lag effect.

Extending these experiments into manipulative experiments in the natural environment has had more variable responses. Explanations for this variability include: some communities are not nutrient limited, ephemeral algal spores are sparse or not available, and that natural communities are more resilient to alterations of the nutrient environment than lab-based communities (Bokn et al. 2003). For eutrophication to affect natural communities in the same way as those in laboratory experiments, it is likely that communities need to be disturbed to create bare space (Valiela et al. 1997, Worm et al. 2002, Kraufvelin 2007). Therefore, the role of increased nutrients together with increased anthropogenic-derived sediments needs to be further clarified with longer term experiments over a wider range of disturbances and established over different seasonal scales to test responses of different algal species.

Based on my short-term experiment, the rocky intertidal zone of the Kaikoura peninsula is resilient to short-term increases in nutrient loads. This is consistent with previous research that predicted resilience unless communities were already perturbed by a disturbance event, either biological, chemical or physical (Thompson et al. 2002, Worm & Lotze 2006). However, numerous other studies have found that eutrophication favours fast-growing macroalgae, such as *Ulva* spp. (Pedersen & Borum 1996, 1997) which alters the recruitment and growth of other macroalgal species (Berger et al. 2003, Raberg et al. 2005). If nutrients are found to have long-term impacts like those seen in mesocosm experiments (Kraufvelin et al. 2006) and other natural ecosystems (Valiela et al. 1997), associated increases in sedimentation are likely to have a two-fold effect. First, sediment particles, especially fine silts, are likely to accumulate nutrients on their surfaces (Chien & Wan 1999) and cause long-term enrichment when the particles are stabilised in algal turfs. Second, if sediment levels have been elevated long-term, the established algal communities are likely to have lower diversity. This can increase susceptibility to subsequent disturbance events (Chapin et al. 2000) and can be further exacerbated if sediments contain seed banks (Santelices et al. 1995) of ephemeral algae such as *Ulva* spp. (Worm et al. 2001).

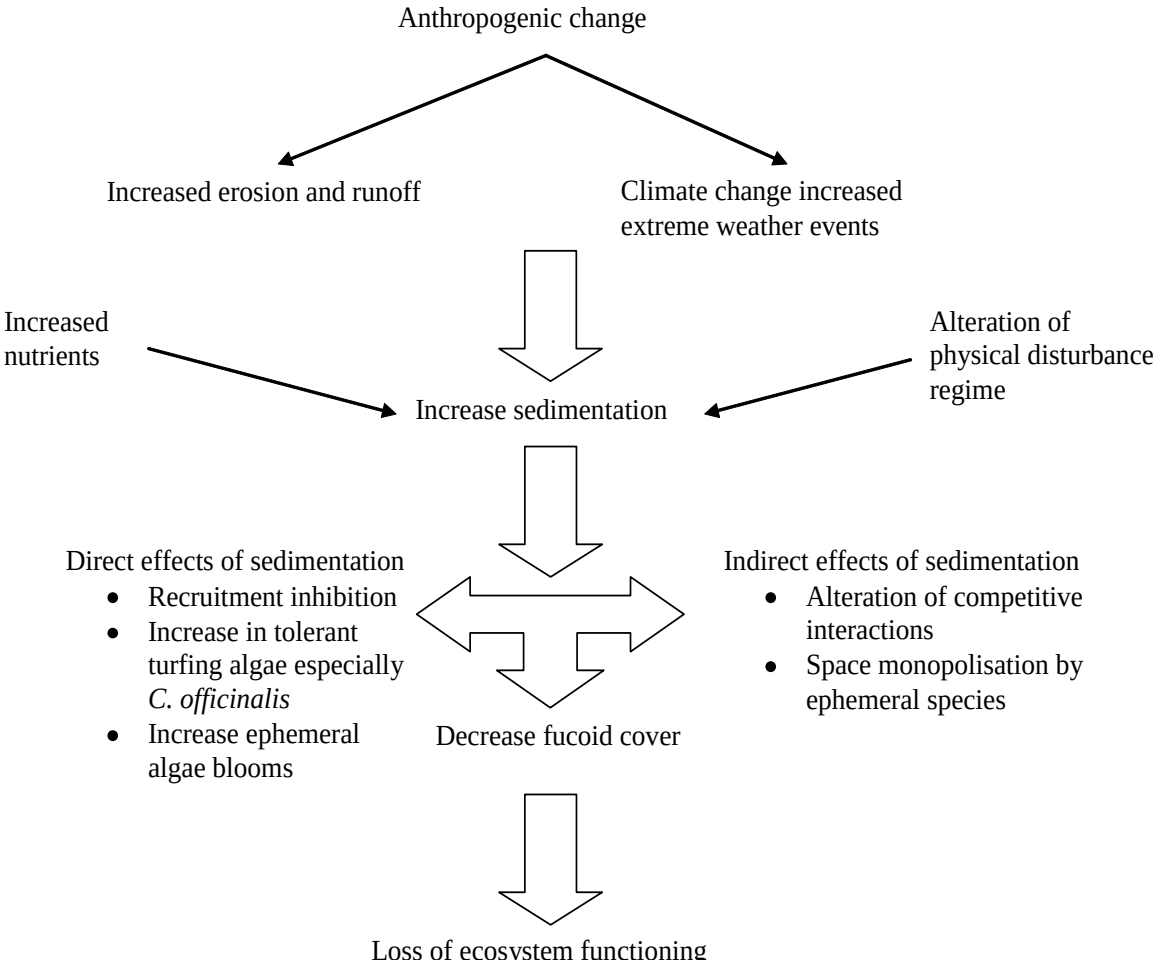


Figure 5.1 Schematic diagram predicting the effects that increased sedimentation will have on rocky shore community structure. Also incorporating the effects of disturbances associated with increased sedimentation, physical disturbance and nutrient addition.

5.5. Future predictions for sedimentation

The increase in sedimentation associated with anthropogenic intrusion into coastal reefs, and possibly with extreme weather events as the climate changes, will result in the loss of canopy-forming algae, and an increased dominance of turf-forming species (Airoldi & Cinelli 1997). My study has shown that this may occur through direct and indirect effects (Fig 5.1). Sedimentation has already increased in many rocky shores worldwide with consequential effects on community structure. The loss of canopy-forming perennial species will be detrimental to entire algal communities, particularly in the mid and upper tidal-zone where they facilitate the presence and abundance of understory species (Hacker & Gaines 1997, Lilley & Schiel 2006). With these processes and effects in mind, policy makers and

environmental managers need to consider actions that reduce direct and diffuse sediment sources and that ameliorate or prevent such advance effects.

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Appendix

1.1 Modified Provalsoli medium recipe (West and McBride 1999)

Disodium DL-b-glycerophosphate pentahydrate	50 g/l
NaNO3	35 g/l
Iron-EDTA (1:1 molar):	600 mg/l
Vitamin B12	25 mg/l
Thiamine	500 mg/l
Biotin	50 mg/l
PII Trace Metals Mix	400 ml
P II Trace Metals Mix (1-litre stock)	
Na^2EDTA	1.0 g/l
Boric Acid (H_3BO_3)	1.12 g/l
Manganese sulfate ($MnSO^{4-}H_2O$)	120 mg/l
Zinc sulfate ($ZnSO^{4-}7H_2O$)	22 mg/l
Cobalt sulfate ($CoSO^{4-}7H_2O$)	5 mg/l